The invertibrate faunas of spartina marshes and their utilization by shorebirds at lindisfarne, Northumberland.

Millard, Andrew Vincent

THE INVERTEBRATE FAUNAS OF <u>SPARTINA</u> MARSHES AND THEIR UTILIZATION BY SHOREBIRDS AT LINDISFARNE, NORTHUMBERLAND

by

Andrew V. Millard

A Thesis presented for the degree of
Doctor of Philosophy in the University of Durham

1976

ACKNOWLEDGEMENTS

I would like to thank Professor D. Barker for allowing me to use the facilities of the Zoology Department, Durham University. I am very much indebted to my supervisor, Dr. P.R. Evans, for his practical assistance, guidance and constructive criticism throughout the project. Thanks are also due to the many other members of Durham University, both staff and students, who gave practical help and advice, particularly P.C. Smith, M. Pienkowski and the M.Sc. Ecology Group of 1973/74. Advice on statistics was kindly given by Dr. G.K. Baggott, of Birkbeck College, London University.

I am grateful to the Nature Conservancy and the Lindisfarne Wildfowl Advisory Committee for allowing me to work on the Lindisfarne National Nature Reserve, and to M.J. Hudson (Deputy Regional Officer), E.F. Pithers and D. O'Connor (Chief Warden, and Warden at Lindisfarne) for practical help and for providing the data presented in Table 33.

Accommodation near Lindisfarne was kindly provided by Mr. and Mrs. J. McDonald, of Low Middleton Farm, to whom I am most grateful. Thanks are due to Mrs. F. Barker, of Leicester University, for typing the final copy. I am grateful to the National Environment Research Council for providing a Research Studentship to finance the project.

Finally, I should like to thank my wife, Susie, for her great assistance and invaluable encouragement at all times.

ABSTRACT

The distributions of the large, mud-dwelling, intertidal invertebrates, and the sediment characteristics were determined within *Spartina anglica* marshes and in adjacent areas of open mud at two sites at Lindisfarne, Northumberland. In an area of fine sediments, *Spartina* marsh had higher carbon, nitrogen, interstitial water and silt/clay contents, and a shallower redox-potential-discontinuity, than adjacent open mud. In an area of coarse sediment no differences were found between sediment characteristics of *Spartina* marsh and open mud. Both total numbers of individual macroinvertebrates, and their species diversity, were greater in open mud at the fine sediment site, but in the *Spartina* marsh at the coarse sediment site. These findings are related to known tolerances of the different species to various physico-chemical parameters.

Detailed studies of *Corophium volutator* and *Hydrobia ulvae* indicated that at the fine sediment site both species were larger within *Spartina* than on open mud. At the coarse sediment site, there was no difference between *Hydrobia* size inside and outside *Spartina*. Densities of both species were inversely related to silt/clay contents above 50%. Not only particle size was implicated in this relationship. Estimates were made of the extent of predation on both species (using exclosures) and of their movements in the field.

Few shorebirds utilised the *Spartina* zone for feeding. Most important was the Redshank (between 28% and 62% of the Lindisfarne population), and second the Dunlin. Major prey taken by Redshank were determined and its effect on the prey estimated at two sites within the *Spartina* zone. These estimates differed from those detected by exclos-

ures because local movements of *Corophium* and *Hydrobia* tended to affect densities within and outside the exclosures.

The utilisation of *Spartina* by shorebirds is related to the corresponding distribution of their known prey species at Lindisfarne. Further spread of *Spartina* would reduce suitable feeding areas for several shorebird species.

CONTENTS

CHAPTER 1. INTRODUCTION

Cord-grass *Spartina anglica* is a common plant in the higher intertidal zones of many mudflats around the British coast. It can spread rapidly both downshore and into established saltmarsh, and has been used widely for reclamation of intertidal land for agriculture (Ranwell 1972). Little is known of the animals associated with it, or of any changes in the composition of intertidal mudflat animal communities resulting from its spread. This thesis describes investigations on the latter topic, and on the effects of loss of mudflats to *Spartina* on the shorebirds which feed in the intertidal zone. The study was carried out on the Lindisfarne National Nature Reserve, Northumberland. Fieldwork was undertaken chiefly between October 1971 and September 1974 inclusive.

i. Origin and spread of Spartina in Britain.

The discovery of *Spartina Townsendi* in 1870 near Southampton and its recognition as a new species is well documented by Huskins (1930) and Marchant (1967). Huskins also discusses circumstantial evidence suggesting that it arose as a hybrid between *S. maritima* and *S. alterniflora*. His cytological evidence supported this theory and further suggested that the original hybrid was a male sterile form, propagating itself vegetatively, and that around 1890 doubling of the chromosome number took place to produce a fertile seed-bearing plant. Marchant (1963, 1967, 1968a, 1968b) re-investigated the cytology of the genus and showed Huskins' original chromosome counts to be incorrect, although his own still supported the hybrid origin and exact parentage of the species.

In 1968 the fertile form was named *Spartina anglica* (C.E. Hubbard 1968). The sterile hybrid *S. Townsendi* H. and J. Groves is now named *S.x. townsendii* H. and J. Groves and the species is known collectively as *S. townsendii* (*sensu lato*).

The rapid natural spread of *S. townsendii* (*s.l.*) along the south coast of Britain, and its subsequent deliberate planting up the east and west coasts of the country as far north as the Cromarty Firth, have been described in detail by Hubbard and Stebbings (1967). They estimated the total area of *S. townsendii* (*s.l.*) around the coasts of Great Britain to be 12,140 ha (29,742 acres), although *S. townsendii* H. and J. Groves is found in quantity only below Hythe in Southampton Water and probably occupies no more than about 20 ha (50 acres) in Great Britain at the present time.

Spartina marsh typically consists of a continuous sward bounded on its seaward side by a zone of isolated clumps. Ranwell (1964b) described the pattern of *Spartina* marsh formation at Bridgwater Bay, Somerset, and estimated that *Spartina* cover in the clump zone increased by about 2% annually. Wilson (1969) found an annual rate of spread of between 3% and 11% on the foreshore at Lytham St. Annes. At the upper levels of the shore, Chater and Jones (1957) estimated that *Spartina* in the Dovey estuary could invade the *Puccinellia* zone at a rate of up to 15 cm per year. It is generally accepted that the downshore extent of *Spartina* marshes does not go beyond levels receiving more than 6 hours submergence in the tidal cycle (Ranwell *et al.* 1964).

ii. Effects of spread of Spartina.

Artificial introduction of *Spartina* followed the realisation that it was able to colonise unstable estuarine mud, accrete silt and hence prevent erosion. Its extensive ramifying rhizome system, together with the stouter vertical anchoring roots and horizontal stolons, accumulate silt particles and raise the marsh level. They are aided by leaves and stems which offer broad surfaces to the silt-bearing tidal water. These also break up the tidal eddies which would otherwise remove the accumulated mud. Ranwell (1964a) measured the accretion rate at Bridgewater Bay, Somerset, over two years and found that up to 10 cm depth of silt accreted per year in high level ungrazed marsh.

Planting of S. townsendii (s.l.) has enabled large areas of land to be reclaimed. The most successful reclamation scheme was the Sloe Dam area of Holland where large scale plantings were started in 1925. By 1950 490 ha (1,200 acres) had been reclaimed (Ranwell 1967). Fears that harbours would be choked by Spartina have largely proved unfounded (Lambert 1964), although some blockage of navigational channels has occurred (Oliver 1920). It is now generally recognised that patchy degeneration of swards, or "die-back", is a consequence of their growth and silt accretion. Detailed investigations of "die-back", and its possible causes, have been made by Goodman (1959, 1960), Goodman et al. (1959), Goodman and Williams (1961), and Sivanesan and Manners (1970, 1972).

iii. Previous work on faunas associated with Spartina.

Little work has been done on the invertebrate faunas of Spartina marshes in Britain. Payne (1972) surveyed the insect fauna of Spartina marshes at Poole, Dorset, and Luxton (1964) examined the zonation of saltmarsh Acarina of the Burry estuary, Glamorgan, some of which are associated with the *Spartina anglica* zone. However there have been no studies of mud-dwelling intertidal invertebrates (e.g. Crustacea, Mollusca and Annelida) within *Spartina* swards.

In the saltmarshes of Georgia, North America, which include *Spartina alterniflora*, extensive faunal studies have been made, particularly of energy flow through the invertebrate populations. Studies of energy flow include those of the mussel *Modiolus demissus* (Kuenzler 1961), the saltmarsh grass-hopper *Orchelimum fidicinium* (Smalley 1960) and a comparison of the latter with the deposit-feeding presobranch *Littorina irrorata* (Smalley 1959a, Odum and Smalley 1959). Other studies associated with the programme included the saltmarsh distribution of Fiddler Crabs (Teal 1958), the relation between insect populations and the growth cycle of *Spartina* and an investigation of arthropod food chains using radioactive tracers (Marples and Odum 1964, Marples 1966).

In North Carolina, studies have been made of the distribution of insects (Davis and Gray 1966) and spiders (Barnes 1953) in saltmarshes which also include species of *Spartina*. R.D. Barnes also investigated the fauna of a *Spartina* marsh drift line (Barnes and Barnes 1954). McMahan *et al.* (1972) compared the microarthropod populations in sewage-exposed and sewage-free *Spartina* saltmarshes.

Other North American studies of invertebrate faunas of *Spartina* marshes include the distribution of the Fiddler Crab *Uca minax* (Kerwin 1971) and the distribution of the saltmarsh snail *Melamysus bidentatus* (Kerwin 1972) in Virginia. On the west coast of North America, Macdonald (1969) made a quantitative study of saltmarsh mollusc faunas including those found in *Spartina* marshes, and Cameron (1972) analysed insect trophic diversity in a *Spartina foliosa* community. Condrey *et al.* (1972) determined the assimilation efficiency of the shrimp *Penaeus setiferus* feeding on the algal mat coating *S. alterniflora*.

Published studies of vertebrates which utilise *Spartina* marshes are also limited, and no investigations have been made of the effect of the spread of *Spartina* on those shorebirds which take intertidal mud-dwelling invertebrates in their diet. Packham and Liddle (1970) list the birds associated with the Cefni saltmarsh, Anglesey, part of which contains an expanding area of *Spartina anglica*. In North America the Laughing Gull (*Larus atricilla*) is known to nest in *Spartina* marshes (Bongiorno 1970), while in Germany the Black-headed Gull (*Larus ridibundus*) has been observed using *Spartina* as a basic nest-building material (Goethe 1968). Reed and Moisan (1971) list the bird species nesting in association with the *Spartina* marshes of the St. Lawrence estuary, Canada, and also these species which use the marsh on migration. Heard (1970) investigated the trematode and cestode parasites of Clapper Rails (*Rallus longirostris*) from *Spartina* marshes in the eastern United States. Butcher (1941) describes how spread of *Spartina* in Great Britain has reduced the area of *Zostera* available to wildfowl.

iv. Purpose of present study.

My study arose from an interest in the rapid spread of *Spartina* in Great Britain and the paucity of literature concerning the effect of its spread on the intertidal fauna. Open intertidal mudflats, which are potential areas for *Spartina* colonisation, house an invertebrate community low in species diversity but often with very high densities of individual species. Apart from the inherent interest in factors controlling distribution and abundance of invertebrate populations, there is an increasing interest in their importance to shorebirds (e.g. Goss Custard 1969, 1970; Hepplestone 1971; Prater 1972). This has resulted from the recent and growing pressure on shorebird feeding grounds from reclamation, industrial development and pollution. The potential loss of feeding grounds has led to studies of their carrying capacities and how these are affected by changes in the populations of important invertebrate species. Complementary to such investigations, it was decided to undertake a broad-based study of the invertebrate faunas of Spartina marshes at Lindisfarne and how they are utilised by wintering shorebirds.

As will be described later, the invertebrate faunas of various Spartina marshes and adjacent areas of open mud were compared to assess the probable consequence of further spread of Spartina, particularly as it might affect those invertebrate species important in the diet of shorebirds. Observations of shorebird feeding behaviour in relation to Spartina distribution were undertaken to complement this study, and possible ways examined in which spread of Spartina might directly affect the invertebrates. This enabled conclusions to be drawn about the likely effect of further spread of Spartina on both the intertidal invertebrates and their avian predators.

v. Content of thesis and rationale of the topics investigated.

The thesis is arranged as follows: -

A description is given in Chapter 2 of the locality in which the study was undertaken. The account includes an assessment of the importance of Lindisfarne to wintering shorebirds and the present extent and history of Spartina in the area. The chapter ends with details of the main study areas selected and the reasons for selecting these areas.

The silt accreted by *Spartina*, together with other sediment characteristics, are important factors affecting invertebrate distribution and abundance. Consequently, to evaluate the effect of *Spartina* on certain invertebrates at Lindisfarne, the relationships between spread of *Spartina* and changes in sediment characteristics are detailed in Chapter 3. The following factors were selected for investigation for the reasons outlined below.

a. Interstitial water content of sediment.

This may be an important factor in determining the distribution of burrowing invertebrates. Both excessively dry and excessively wet conditions may hinder the construction or maintenance of burrows. Gee (1961) found that the distribution of *Corophium arenarium* was restricted by water content and suggested that too high a water content may prevent satisfactory burrowing.

b. Depth of redox-potential-discontinuity.

Fenchel and Riedl define the transition from the oxidised surface layer of sediments to the underlying reduced sulphide layer as the redox-potential-discontinuity (R.P.D.). The origin of, and conditions within, the reduced sulphide layer are discussed by Perkins (1957), Fenchel and Riedl (1970) and Eltringham (1971). The depth of the R.P.D. is known to affect the distribution of invertebrate populations and Fenchel and Riedl (1970) detail those animals which can survive below it in the reduced sulphide layer.

c. Salinity.

Salinity is an important factor affecting the distribution particularly of estuarine animals (Green 1968) and mud-dwelling intertidal animals (Eltringham 1971).

d. Carbon content of sediment.

Sources of carbon in littoral sediments include both live micro-organisms and dead organic detritus. The live organic material consists mainly of bacteria, an important food source for deposit-feeding invertebrates (Newell 1965). However, Meyer (1973) concluded that large amounts of detritus produce a reduction in the density of diatoms (another possible food source), possibly by obscuring the light from them. Therefore the total carbon content of sediment provides one measure of the potential food available to invertebrates.

e. Nitrogen content of sediments.

Newell (1965) attributed high nitrogen content in sediments to high micro-organism densities and Meyer (1973) demonstrated that 50% of the variation in sediment nitrogen at Lindisfarne was associated with variation in viable aerobic bacteria (the rest was probably associated with anaerobic and dead bacteria). Hence nitrogen content provides a second measure of potential food resources available to deposit- and suspension-feeding invertebrates.

f. Particle size.

Newell (1965) correlated increasing silt/clay content with an increase in Hydrobia ulvae density. He concluded that the large surface area per unit volume of small particles allowed greater micro-organism populations to exist, thus providing more food for deposit-feeders. Meadows (1964) demonstrated that Corophium volutator prefers to burrow in sediment with smaller particle sizes. Fenchel and Riedl (1970) partly associated an increased silt/clay content with a raising of the R.P.D. towards the sediment surface. In view of these findings, particle size was investigated and correlation graphs of silt/clay content with carbon and nitrogen content, and depth of R.P.D. are presented.

Chapter 4 is a general survey of the densities of various invertebrate species inside and outside areas of *Spartina*, both in summer and winter. Sources of variation in invertebrate densities were investigated first to decide upon the best sampling programme. Summer and winter densities for dominant invertebrate species from two main sites at Lindisfarne are presented. These are supplemented with the results of two additional surveys to give an overall picture of invertebrate distribution in *Spartina* marshes at Lindisfarne.

The relationship between the distribution of certain invertebrates and distribution of *Spartina*, detailed in Chapter 4, was investigated further to find out how *Spartina* might control the distribution of these invertebrates. Two of the commonest species (*Corophium volutator* and *Hydrobia ulvae*) were selected for this study because of their relatively wide distribution and their importance in the diet of shorebirds (particularly of the Redshank, *Tringa totanus*). Results are presented in Chapters 5 and 6. In both species the mean size and mean dry weight of animals inside and outside *Spartina* were compared to determine any differences in growth rate. The relationships between densities of the species and silt/clay content of the sediment were determined to assess the effect of the high silt/clay content found in *Spartina* on the two species. The behavioural response of *Corophium* to sediment within *Spartina* was studied and compared with that on open mud. An attempt was made to determine the effect of predation on both species by use of exclosures. Differing predation rates inside and outside *Spartina* are a potential cause of differing densities and size distributions of the invertebrates. Since movements of the species could affect the exclosure results, a study was made of the distance moved by both species during a small number of tidal cycles. Studies of *Hydrobia* movement were made both in the *Spartina* areas and on the open mud; but studies of *Corophium* movement were restricted to the open mud because of its low density within *Spartina*.

Chapter 7 considers how the spread of *Spartina* has affected wintering shorebirds at Lindisfarne. Moreover, since this thesis is concerned with factors affecting the distribution and abundance of invertebrates in *Spartina* marsh, there is a need to investigate the effect of shorebirds as predators of these invertebrates. Consequently this chapter discusses firstly, those species of shorebirds which were found most often in areas colonised by *Spartina*, and secondly, to what extent the birds utilised these areas by choice or necessity. Finally, the predation pressures exerted by the birds on the invertebrates have been estimated for comparison with the results of population changes of invertebrates within the exclosures (Chapters 5 and 6).

Detailed discussion of the data is deferred to Chapter 8. The form of *Spartina* occurring at Lindisfarne is *S. anglica* and is referred to as *Spartina* throughout the text. When first introduced, invertebrate species are referred to by their specific names and thereafter only by their generic names. Specific names of birds encountered in this study are given in Table 26, p 86.

Abbreviations used in the thesis are as follows: -

EHWS - extreme high water springs tidal level

MHWS - mean high water springs tidal level

MHWN - mean high water neaps tidal level

S.E. - standard error

Probability values of 5% or less are taken as significant.

CHAPTER 2. STUDY AREA

i. Description.

The Lindisfarne National Nature Reserve is situated on the north Northumberland coast, approximately 80 km (50 miles) north of Newcastle-upon-Tyne. The immediate hinterland is agricultural land with some low moorland (approximately 180 m high). The Cheviot hills (approximately 800 m high) are situated about 16 km to the west. Berwick-upon-Tweed (12,000 inhabitants) is the nearest town, about 13 km to the north. The nearest industrial areas are Tyneside to the south and Edinburgh which is about 150 km to the north.

Lindisfarne (Fig. 1), which was designated a national nature reserve in 1964, covers an area of about 3,000 ha (12 sq.miles), consisting mainly of intertidal mud- and sandflats, saltmarsh and sand dunes. It is famous particularly for wintering wildfowl and shorebirds, although some good examples of dune flora are found on Holy Island. Shooting by permit is allowed on the main flats, but is prohibited on the two wildfowl refuges, Budle Bay and Goswick Sands. Mussel collecting by permit takes place in Budle Bay, but did not affect my study.

ii. Importance to birds.

Lindisfarne occupies an important geographical position for shorebirds, the nearest comparable estuaries being the Forth (80 km North) and Teesmouth (130 km South), both of which are threatened by reclamation, industrialisation and pollution. Accounts of wader movements on Fenham Flats (Fig. 1) are given by Chapman (1907), Perry (1946) and Brady (1949). Recent maximum winter wader counts by the Nature Conservancy have included 22,000 Dunlin (<u>Calidris</u>

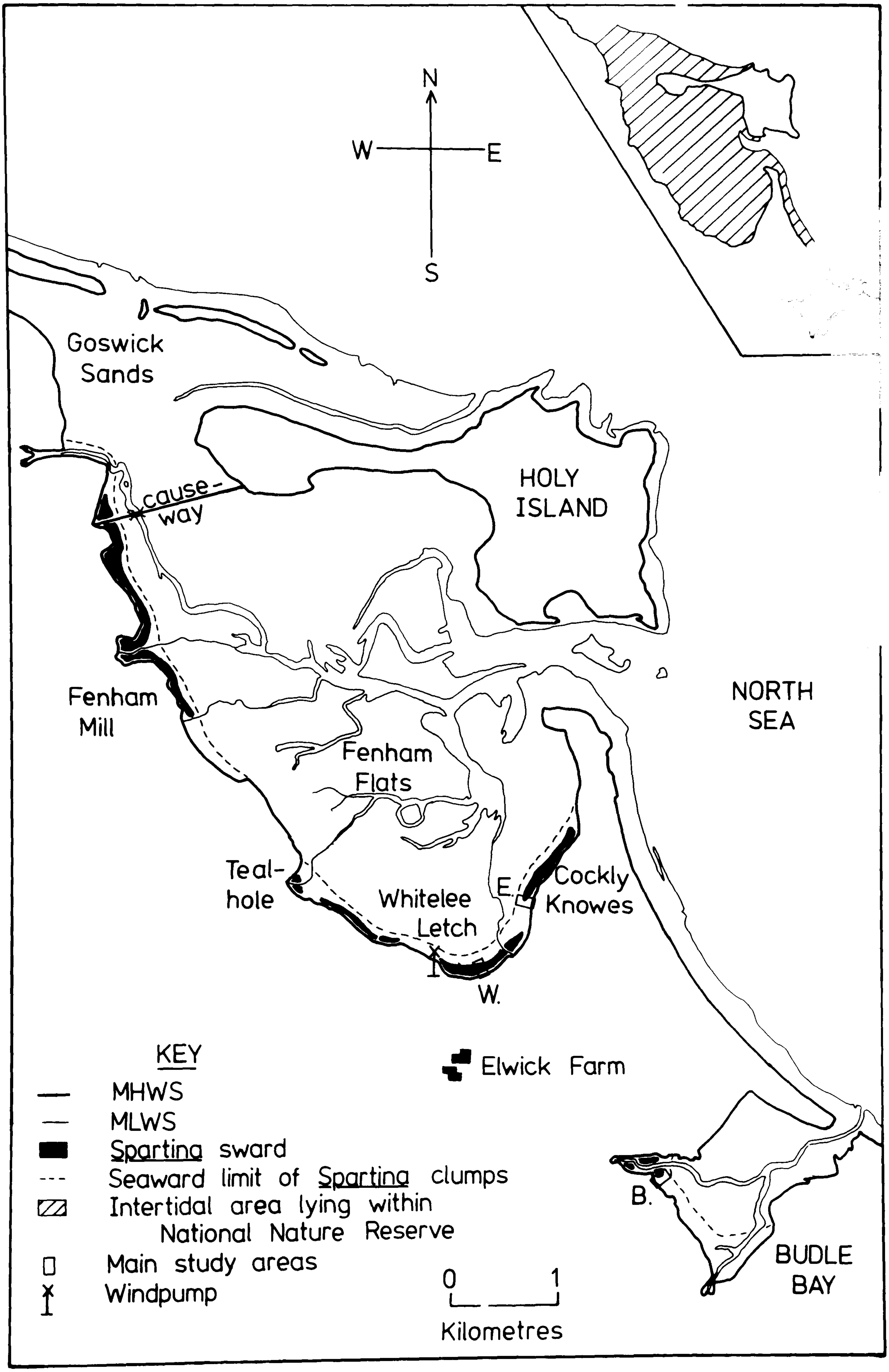


Fig. 1. Lindisfarne National Nature Reserve.

alpina) and 6,700 Bar-tailed Godwit (Limosa lapponica) in 1973/74, and 11,000 knot (Calidris canutus) and 1,300 Redshank (Tringa totanus) in 1972/73. Lindisfarne is well known also for its wildfowl and is a popular wildfowling area for the North-East. In the winter 1970/71 maximum wildfowl counts included 27,000 Wigeon (Anas penelope), 1,000 Pale-bellied Brent Geese (Branta bernicola) and 430 Whooper Swans (Cygnus cygnus). The importance of the area is emphasised by the total sum of the maximum counts of all shorebird species in 1970/71 (33,320), which ranked the area eleventh in importance amongst British estuaries. It is recognised as a Wetland of International Importance under the Ramsar Convention.

iii. Spread of Spartina.

Spartina was first planted at Lindisfarne in 1929 at a site adjacent to the windpump (Fig. 1). Since then it has spread considerably. Hubbard and Stebbings (1967) estimated that it occupied an area of about 36 ha in 1963. Using aerial photographs taken in 1969, I estimated the total area of Spartina at Lindisfarne to be about 40 ha. Current distribution of Spartina is given in Fig. 1. Clearly, recent spread has been maintained so that it now occupies much of the zone between MHWS and 200 m downshore on the landward side of the Reserve.

In some areas, particularly Elwick-Whitelee Letch and near the Causeway, extensive swards have developed. Beyond these, 'pioneer' clumps are found, which decrease in number downshore until the limit of Spartina growth is reached at between 200 m and 300 m below MHWS. There is also variation in Spartina growth alongshore. Both the density and height of culms varies, often in accordance with the type of sediment. At Whitelee Letch, where the sediment is very fine and soft, the culms appear taller with a higher density than at Cockly Knowes, where the sediment is coarser and firmer. Chater and Jones (1957) suggested that sand causes stunted growth of Spartina. However, Spartina is known to grow well on sediments ranging from clays to gravels, although maximum heights, of over 1 m, are found on silts. Braybrooks (1957) concluded that the degree of shelter was important to Spartina growing on a sandy sediment. The variation in shelter at Lindisfarne may well account for the differing forms of Spartina growth.

During the course of this study, the recent increase in the rate of spread of Spartina seemed to be maintained. I noted the appearance of new clumps in hitherto uncolonised areas, and an increase in the density of clumps in existing areas. It seems likely that this will continue unless action is taken to curb its spread.

iv. Selection of study areas.

An ideal study of the effect of spread of Spartina on intertidal invertebrates would require the monitoring of changes over several years in the invertebrate populations of an area as Spartina spread across it. Since limitations of time prevented this form of study, it was decided to compare areas already colonised by Spartina with adjacent areas at an equivalent tidal level, areas which differed only, as far as possible, in being free of Spartina. Using this criterion, two sites were selected (Fig. 1), one in an area of fine sediment and vigorous Spartina growth at Budle Bay (Site B), and one in an area of coarser sediment and more stunted Spartina growth at Elwick-Cockly Knowes (Site E). The majority of invertebrate studies were carried out at these two sites, although subsidiary studies were made at Elwick-Whitelee Letch (Site W), Fenham Mill and Teal Hole.

Site B is shown in Fig. 2, together with the position of transects, exclosures, and the bird observation area. The site consists of three well defined areas; a dense sward of *Spartina*, an area of *Spartina* clumps interspersed with patches of open mud, and an area of open mud. The density of *Spartina* within the sward was measured by counting the number of culms in at least 100 10 cm x 10 cm random quadrats and found to be 238 $\pm$ 23.4 (S.E.) per m^2. Between MHWN and EHWS lies a saltmarsh community penetrated by many ramifying creeks. To the north west of the site is a freshwater burn, Ross Low. The area is relatively undisturbed by humans during the winter months.

Site E is shown in Fig. 3, together with the position of the two transects. The site consists of a southern area of open muddy sand and a northern area of *Spartina* clumps interspersed with patches of open muddy sand. The mean density of *Spartina* within the larger clumps was found to be 162 $\pm$ 21.9 (S.E.) culms per m^2. Upshore of the site is a track running parallel to the shore and then an extensive area of sand dunes. From September to February the area is frequented by wildfowlers.

The extensive area colonised by *Spartina* at Lindisfarne provides a variety of conditions for wintering shorebirds. In particular, different areas may vary in the type of prey and shelter offered to the shorebirds. Consequently, two contrasting sites were selected for observations of shorebirds feeding in association with *Spartina*. Site B at Budle Bay (described above) was selected as a relatively sheltered area, free from wildfowling disturbance and known to contain *Corophium volutator*, a potentially important prey

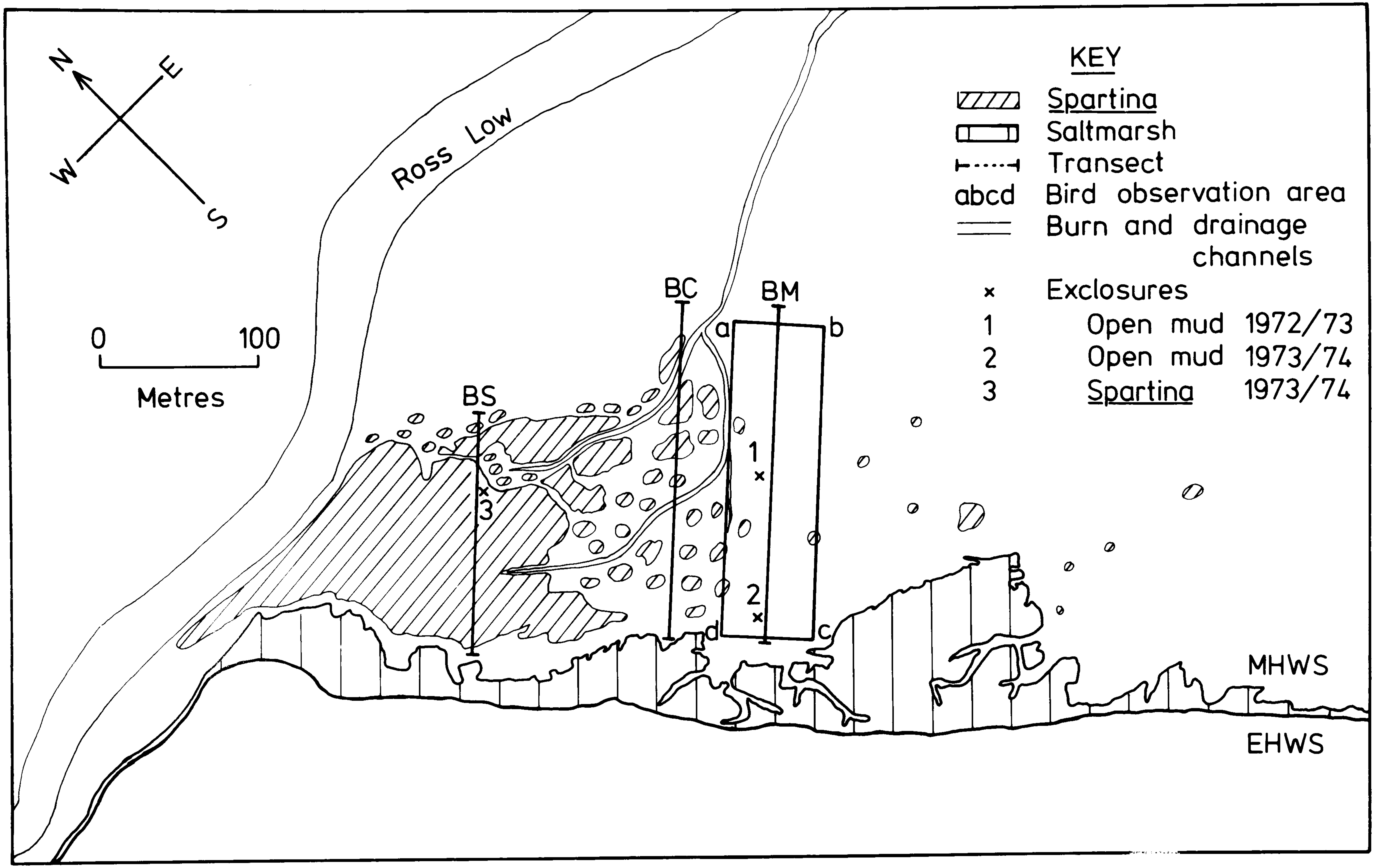


Fig. 2. Site B (Budle Bay).

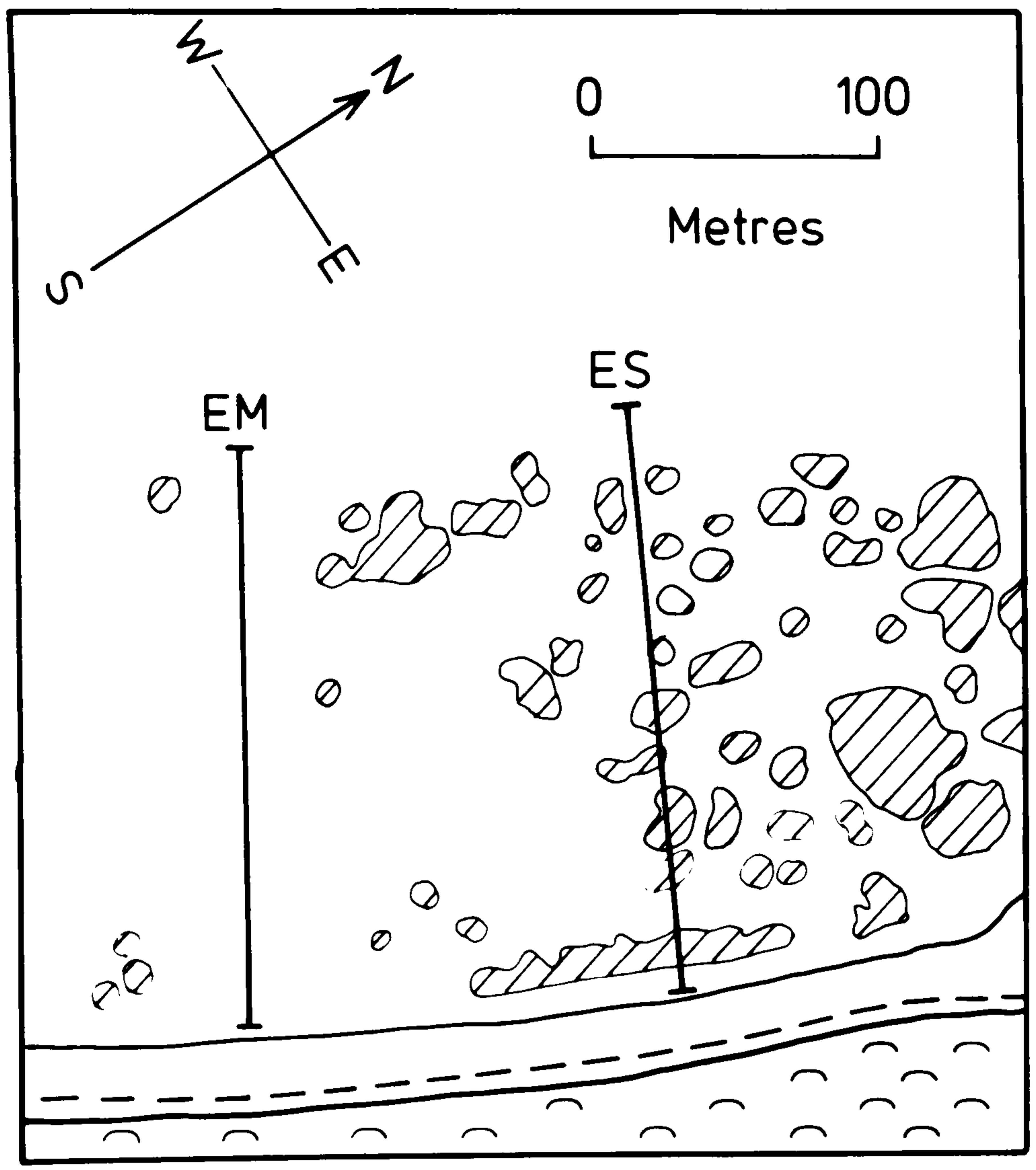


Fig. 3. Site E

(Elwick - Cockly Knowes).

KEY to Figs. 3 and 4.

Spartina
Sand dunes
Transect
efgh Bird observation area
× Exclosure open mud 1972/73
Track
MHWS
EHWS

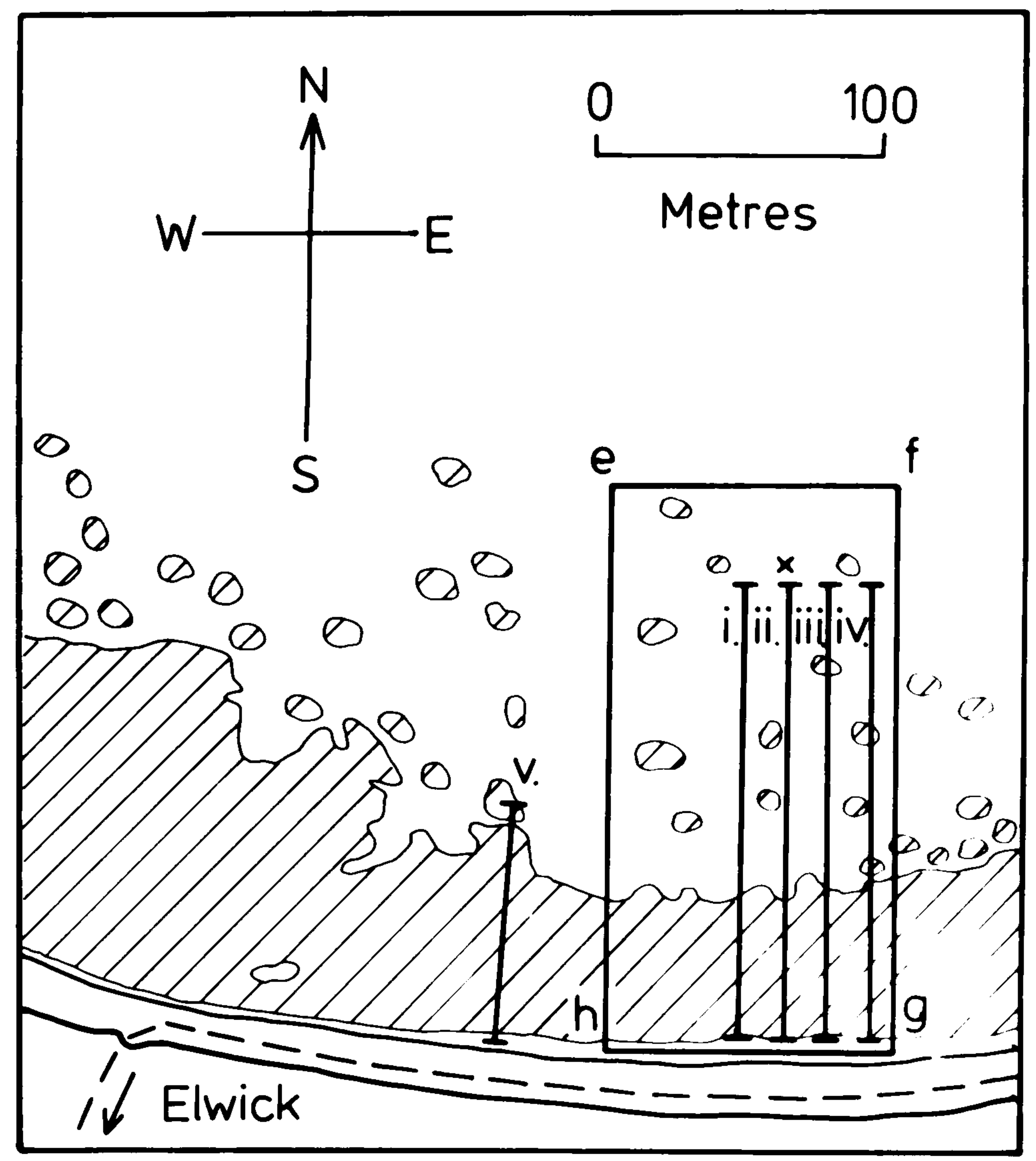


Fig. 4. Site W

(Elwick - Whitelee Letch).

item. Site W at Elwick-Whitelee Letch (Fig. 4) was selected as a more exposed area where wildfowling occurs and Corophium is known to be absent from the very fine sediment. A dense Spartina sward extends downshore from MHWS for about 50 m. Beyond this are Spartina clumps, progressively decreasing in density downshore. Upshore of the sward is a track, continuing round the coast to Site E, and a low bank about 2 m high. In addition to shorebird observations, this site was also used for a subsidiary study of the invertebrate fauna of Spartina (Chapter 4, iii) and a study of variation in invertebrate density (Chapter 4, ii).

Relevant details of the minor study areas, Teal Hole and Fenham Mill, are given in the appropriate section.

CHAPTER 3. THE EFFECT OF THE PRESENCE OF *SPARTINA* ON SEDIMENT CHARACTERISTICS

i. General method.

Measurements of each characteristic were made at a number of sampling stations along the three transects at Site B (Fig. 2), and the two transects at Site E (Fig. 3), and thus gave information on the sediment characteristics, both in areas of *Spartina* and in adjacent areas free of it. Individual samples were labelled according to the transect from which they were taken, and the distance, in metres, of the station from MHWS, e.g. ES 150.

ii. Presentation of results.

At both Sites B and E, the results from the transects through open mud (transects BM and EM) were analysed for the presence or absence of a trend along each transect in the values for each sediment characteristics. Any such trend was detected by calculating the value of the gradient (b) and then testing it for significance as illustrated below. A relationship of the type:

sediment characteristic (y) = b. distance from MHWS (x) + c

was assumed.

e.g. Salinity - Transect BM

Dissolved salts in g per kg of seawater. (y)	Distance from MHWS (m) . (x)
37.46	0
36.00	30
36.00	90
33.80	150
34.54	210

sum of y = 177.80   sum of x = 480

sum of y^2 = 6330.70   sum of x^2 = 75600

sum of xy = 16643.4

$$\text{Gradient } b = \frac{\left[\text{sum of } xy - \dfrac{(\text{sum of } x)\ (\text{sum of } y)}{n}\right]}{Sx^{2*}}$$

$$b = \frac{16643.4 - 17068.8}{75600 - 46080}$$

$$= \underline{-0.014}$$

$$\text{Standard error of slope } (SE_b) = \sqrt{\frac{Syx^{2**}}{Sx^2}}$$

$$\therefore SEb = \sqrt{\frac{0.657}{29530}}$$

$$= \underline{0.00469}$$

Test of significance: -

$$t_{(n-2)} = \frac{b}{SE_b}$$

$$= \frac{0.014}{0.00469}$$

i.e. $t_3 = 2.985$, $p > 0.05$

$\therefore$ no trend was present.

$$*Sx^2 = \text{sum of } x^2 - \frac{(\text{sum of } x)^2}{n}$$

$$Sy^2 = \text{sum of } y^2 - \frac{(\text{sum of } y)^2}{n}$$

$$**Syx^2 = \frac{Sy^{2*} - \left[\dfrac{\left(\text{sum } xy - \dfrac{(\text{sum } x)\ (\text{sum } y)}{n}\right)^2}{Sx^2}\right]}{n - 2}$$

In the absence of a trend for any chosen factor, the mean and standard deviation of the values from the open mud ('baseline') transect were calculated. Samples from the other adjacent transects were then compared with the baseline mean by calculating t for each sample as shown: -

$$t = \frac{d}{\sigma}$$

where d = difference between sample and baseline mean.

σ = standard deviation of baseline transect.

t was then looked up in Student's t distribution table at n - 1 degrees of freedom. This technique tends to underemphasise any difference that may exist and is thus a more powerful test than comparing pairs of samples at equivalent tidal levels.

iii. Interstitial water content of sediment.

Samples were collected on 25/7/74 between 3 and 7 hours after high water. At each station a glass tube, 13 cm long and 2.6 cm in diameter, was screwed into the mud and a rubber bung inserted into the top. The tube was then screwed out and another bung inserted into the bottom. This procedure was used by Fraser (1932), Stopford (1951), Southward (1953), and Gee (1961). The depth of water above the sediment in the tube was noted, together with the depth of the R.P.D. (see iv. below). The tube contents were then emptied into a watertight jar and returned to the laboratory. After initial weighing, the mud was dried at 105°C. for 48 hours and then reweighed.

The depth of water overlying the sediment varied considerably throughout the area. To make meaningful comparisons of the interstitial water, the weight of water overlying the sediment in the tube (calculated from the volume measured) was subtracted from the weight of water found by drying.

Results (Fig. 5 & Table 1): -

Results from within Spartina at Site B gave interstitial water contents significantly higher than the mean for the baseline transect, the highest percentages occurring within the dense sward of transect BS. At Site E no significant differences were found between the water contents of the two Spartina samples (ES 60 and ES 90) and the mean for the baseline transect. The high value for sample ES 0 may have resulted from freshwater runoff from land immediately behind the shore, and the low value for sample ES 150 from an anomaly in the drainage pattern of the sediment.

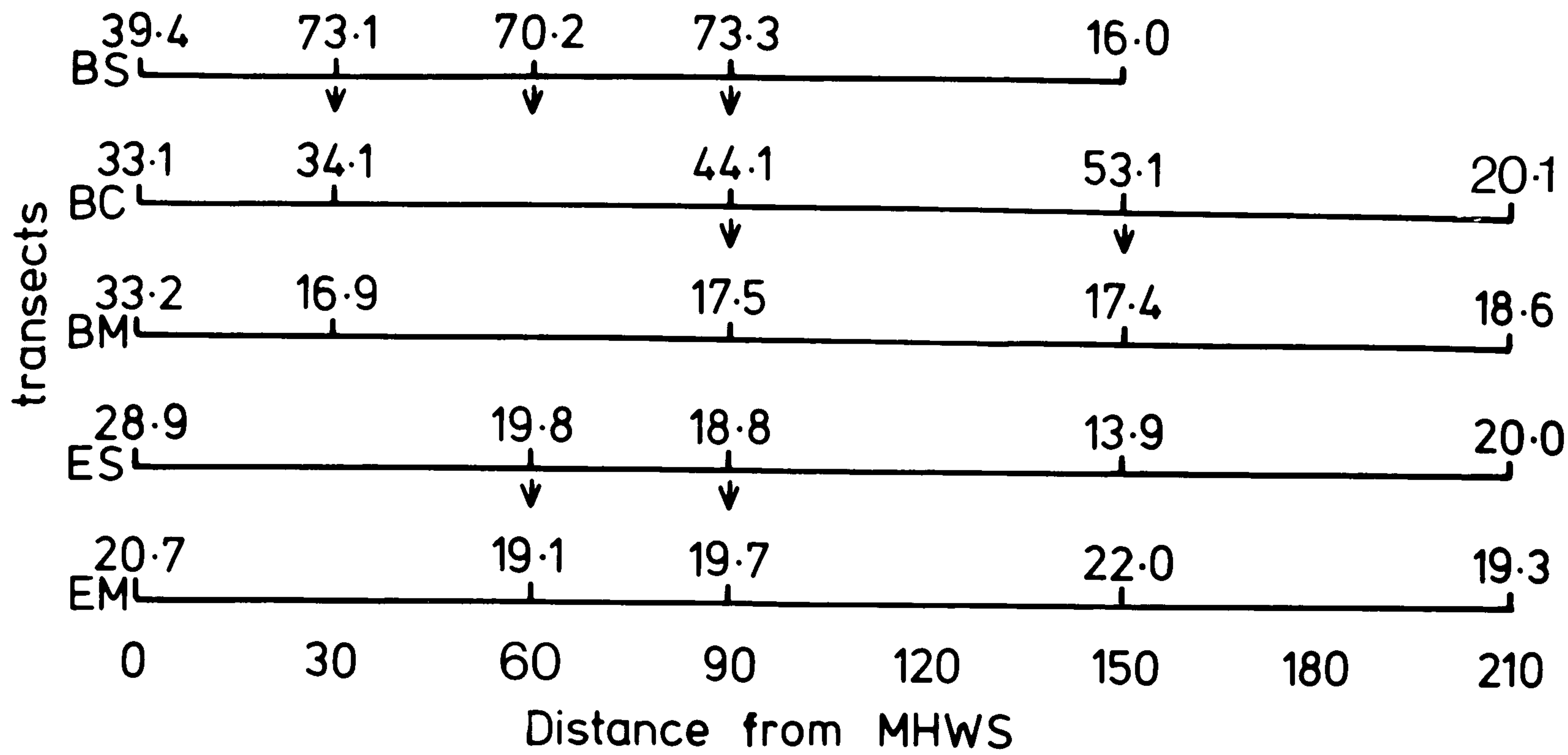
iv. Depth of redox-potential-discontinuity.

Measurement of the depth of the R.P.D. was made during the collection of samples for estimation of interstitial water content, described in iii. above.

Results (Fig. 6 & Table 2): -

Statistical analysis revealed a gradient in transect BM and it was therefore not possible to compare individual samples in transects BS and BC with a baseline mean. However, it is clear by inspection of the results that the depth of the R.P.D. in transect BS was considerably less, particularly within the Spartina, than that found in the open mud. Also, in transect BC, sample BC 90 had a relatively shallow R.P.D., while towards the shore, the depth of the R.P.D. was less than in the corresponding section of transect BM.

At Site E no gradient existed in the depth of the R.P.D. in transect EM and a direct comparison was made between individual samples of transect ES and the baseline mean. Surprisingly,

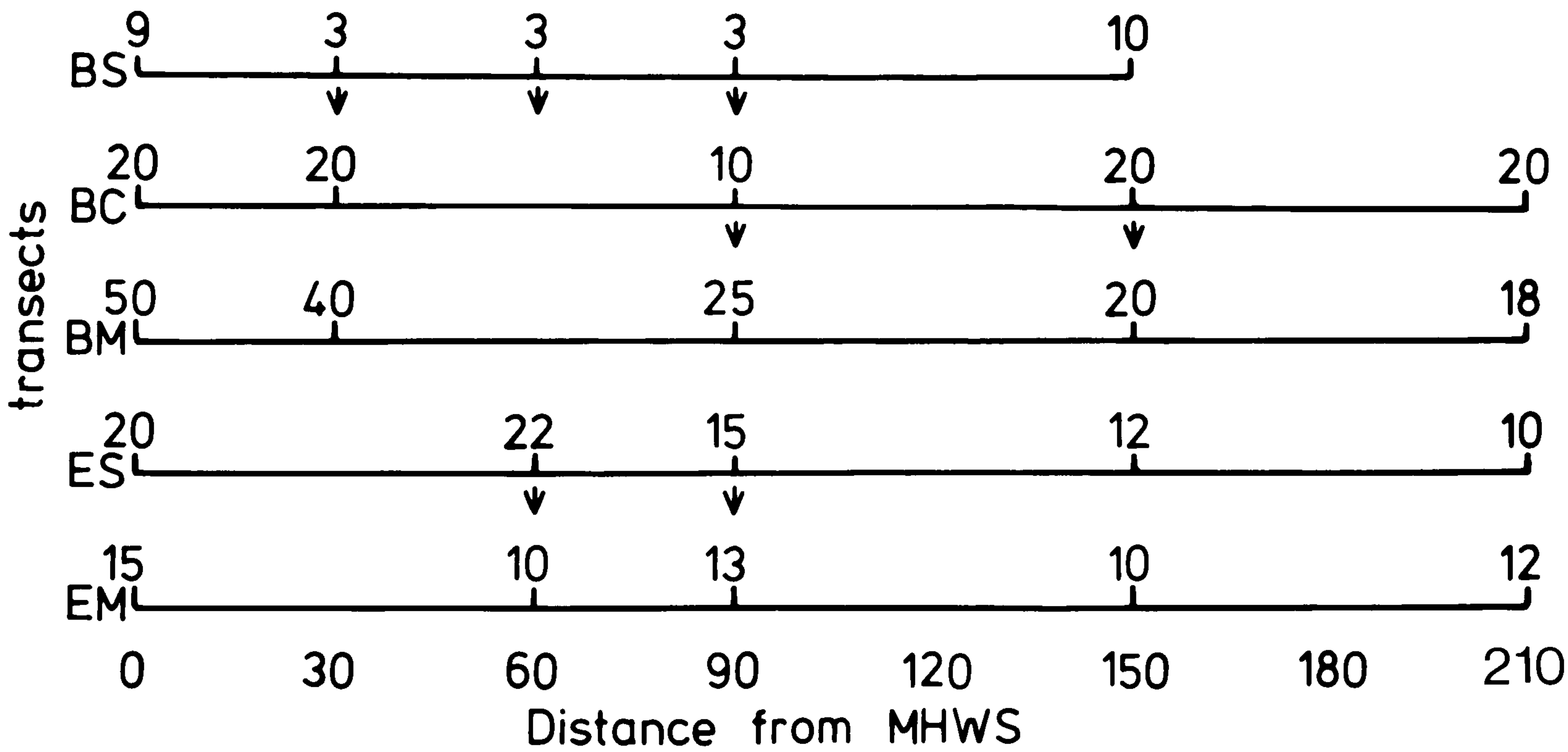


t(BM) = 1·172, P > 0·1. ∴ no trend. Mean = 20·72

t(EM) = 0·043, P > 0·1 ∴ no trend. Mean = 20·16

↓ = sample from within Spartina

Fig. 5. Interstitial water as a percentage of sediment wet weight.



t(BM) = 4·635, P < 0·02. ∴ trend present.

t(EM) = 0·952, P > 0·1. ∴ no trend. Mean = 12·0

↓ = sample from within Spartina.

Fig. 6. Depth of redox-potential-discontinuity (in millimetres).

TABLE 1

Comparison between interstitial water content values from the three *Spartina* transects (BS, BC and ES) and their appropriate 'baseline' means (from transects BM and EM). Samples from within *Spartina* swards or clumps are indicated thus *.

Sample	t	Significance level
BS 0	3.051	0.05
BS 30*	8.369	0.01
BS 60*	7.906	0.01
BS 90*	8.401	0.01
BS 150	0.754	ns
BC 0	1.981	ns
BC 30	2.140	ns
BC 90*	3.785	0.05
BC 150*	5.175	0.01
BC 210	0.096	ns
ES 0	8.153	0.01
ES 60*	0.336	ns
ES 90*	1.269	ns
ES 150	5.840	0.01
ES 210	0.149	ns

ns = not significant

TABLE 2

Comparison between depth of redox-potential-discontinuity values from transect ES and the 'baseline' mean from transect EM. Samples from within *Spartina* clumps are indicated thus *.

Sample	*t*	Significance level
ES 0	4.217	0.05
ES 60*	5.271	0.01
ES 90*	1.581	ns
ES 150	0	ns
ES 210	1.054	ns

ns = not significant

two samples had R.P.D.s significantly deeper than the baseline mean, one from within Spartina (contrasting with the situation at Site B) and the other (sample ES 0) associated with freshwater runoff, which presumably resulted in better oxygenation.

v. Salinity.

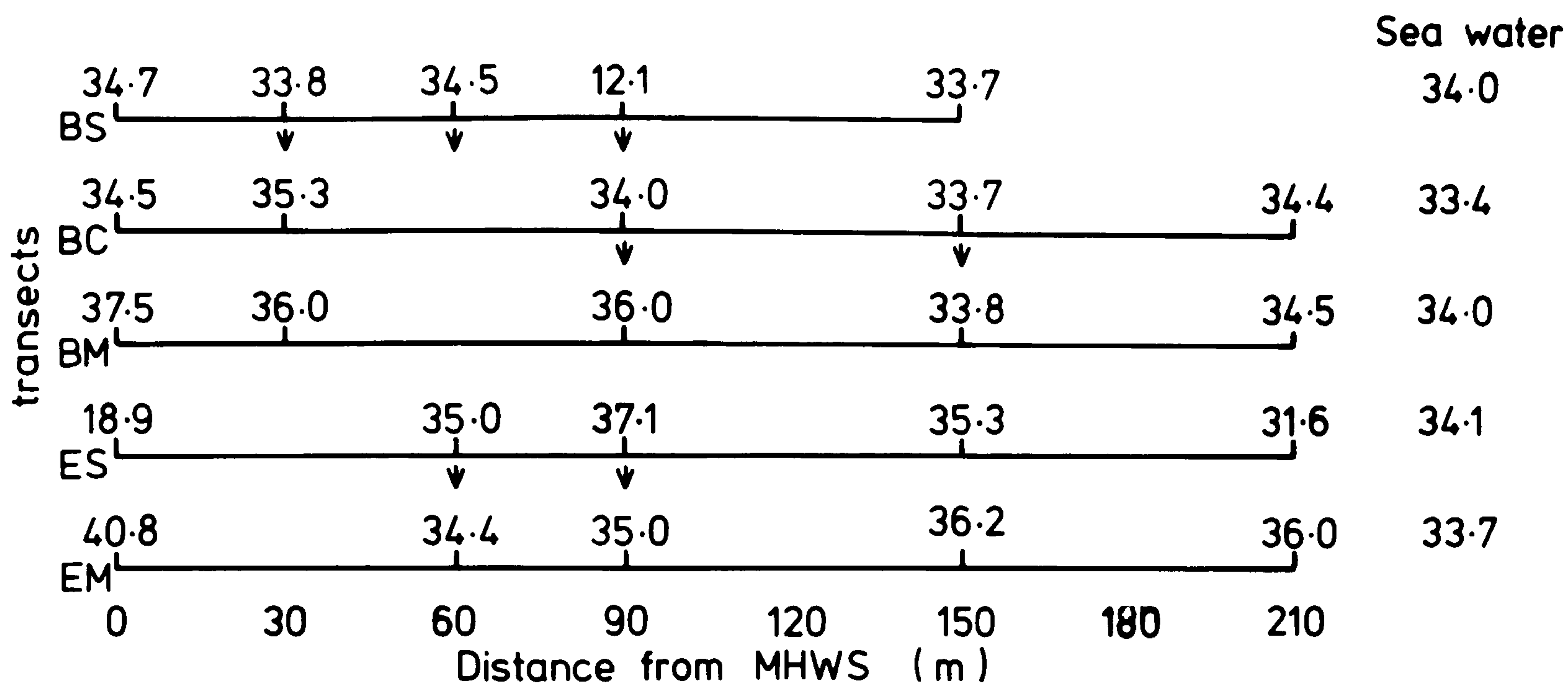
Sampling of the sediments was carried out at both Sites B and E on 18/7/74 immediately before high water. A sample of seawater was also taken from the incoming tide just before it covered the study area. In this way, external conditions affecting the salinity of the interstitial water had the maximum possible time (one low tide period) in which to act before normalisation by the sea occurred.

Samples of mud measuring 10 cm x 10 cm were collected to a depth of 5 cm and taken to the laboratory in sealed polythene bags. The interstitial water was separated from the sediment by vacuum filtration, and transferred to a 2" x 1" specimen tube which was then sealed.

The salinity was determined later by titration against 0.3N silver nitrate using potassium dichromate indicator, as described by Strickland and Parsons (1960 - Low Precision Method). Three determinations were made for each sample and the mean chlorosity calculated. Salinity values were obtained from the chlorosities by referring to the table given by Strickland and Parsons (1960).

Results (Fig. 7 & Table 3): -

Only sample BS 90 at Site B differed significantly from the baseline mean and was much lower than the value for seawater. Since the depth of the R.P.D. at this station was only 3 mm it is



t (BM) = 2·985, P > 0·05. ∴ no trend. Mean = 35·6

t (EM) = 0·130, P > 0·1. ∴ no trend Mean = 36·5

↓ = sample from within Spartina.

Fig. 7. Salinity (g of dissolved salts per kg of sea water).

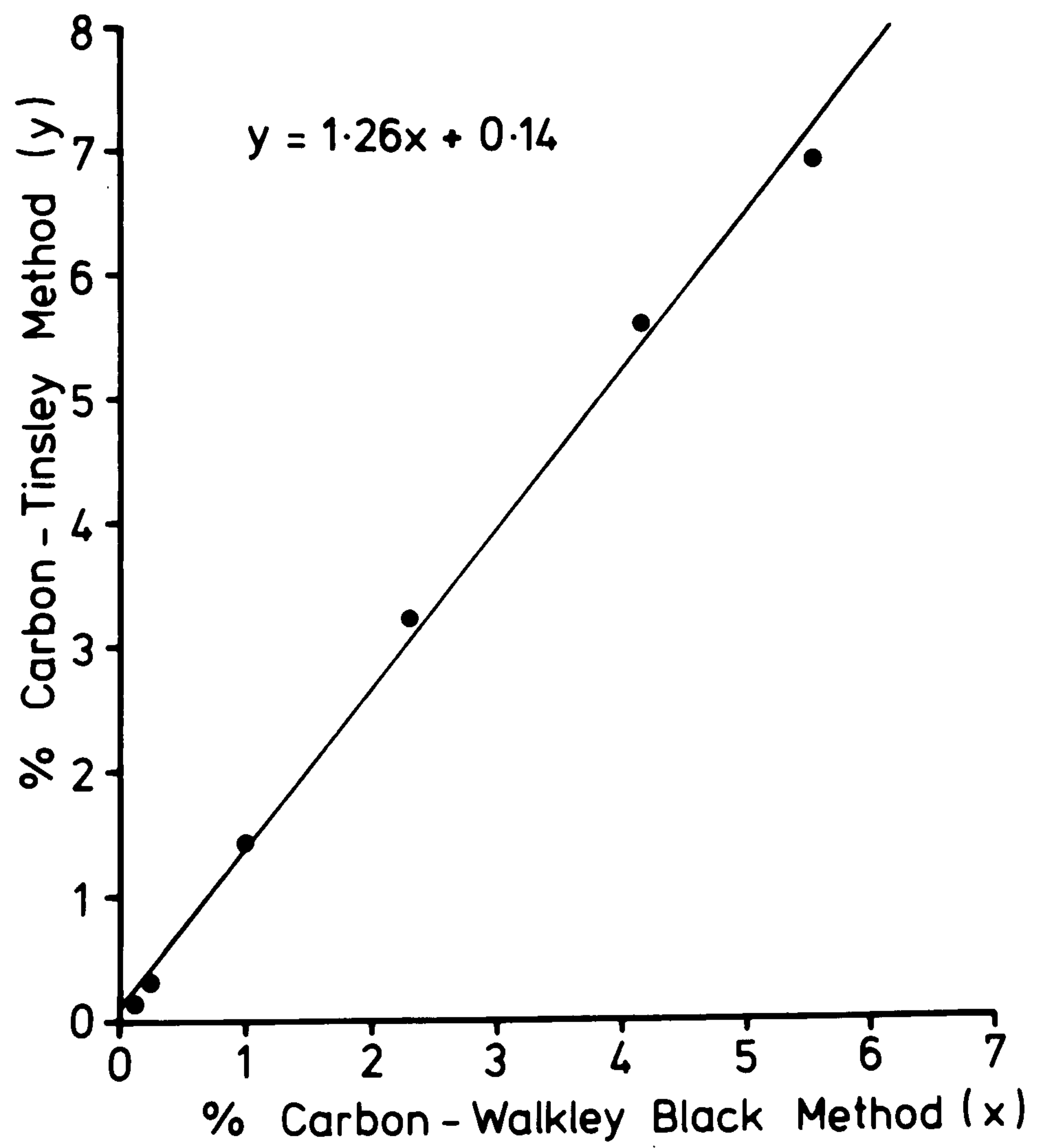


Fig. 8. Calibration graph for correction of Walkley Black carbon estimations.

TABLE 3

Comparison between salinity values from the three *Spartina* transects (BS, BC and ES) and their appropriate 'baseline' means (from transects BM and EM). Samples from within *Spartina* swards or clumps are indicated thus *.

Sample	*t*	Significance level
BS 0	0.689	ns
BS 30*	1.378	ns
BS 60*	0.799	ns
BS 90*	18.390	0.001
BS 150	1.480	ns
BC 0	0.799	ns
BC 30	0.219	ns
BC 90*	1.253	ns
BC 150*	1.480	ns
BC 210	0.908	ns
ES 0	7.638	0.01
ES 60*	0.650	ns
ES 90*	0.303	ns
ES 150	0.516	ns
ES 210	2.107	ns

ns = not significant

unlikely that the low salinity was due to freshwater seepage through the sediment. It is possible that freshwater retention occurred below the surface when the tide ebbed.

At Site E only sample ES 0 differed from that of the baseline mean, being significantly less. This provided further evidence of freshwater runoff from the dunes behind.

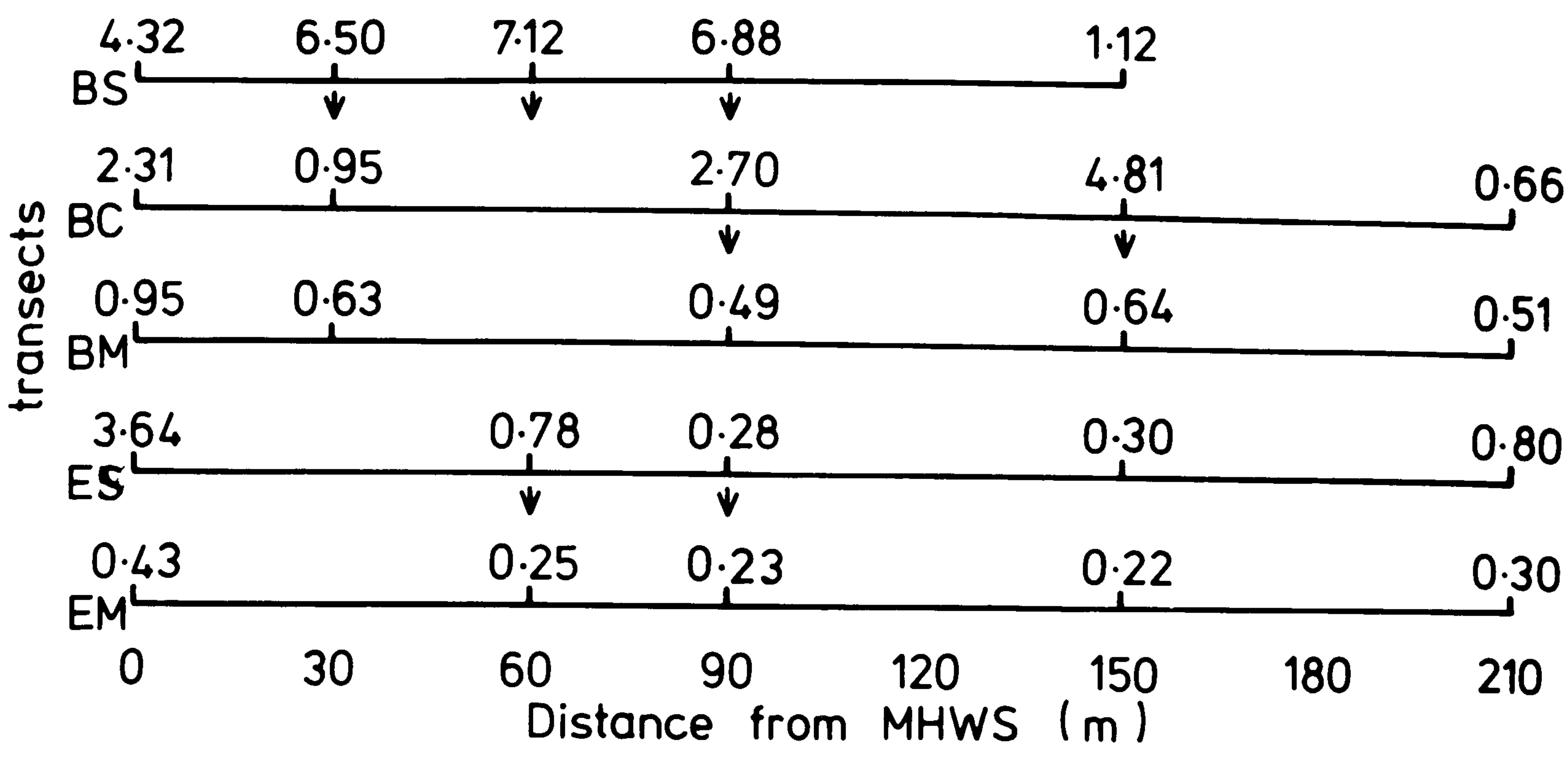
vi. Carbon content of sediment.

Samples for carbon analysis were collected on 13/8/73 at Site B and 29/8/73 at Site E from the top 1 cm of sediment by dragging a mud sledge (Capstick 1957) across the mud surface for approximately 10 cm. Three samples of the surface mud were obtained in this way from each station and mixed together thoroughly in a polythene bag which was subsequently sealed.

In the laboratory the samples were oven dried at 105°C for 48 hours. Between 0.5 g and 1.0 g of dried sediment was ground to a fine powder in a mortar and analysed for carbon using the Walkley Black Wet Oxidation Method (Appendix 1, p 134). This method effects approximately 75% recovery of carbon. Higher recovery (approximately 95%) is ~~effected~~ achieved by the more lengthy Tinsley modification of the method (Appendix 1, p 134) which employs direct heating. To check on the validity of the unmodified method used in 1973, six samples were collected on 8/7/74 and analysed for percentage carbon by both methods. From these results a calibration curve was plotted (Fig. 8) to enable carbon values obtained by Walkley Black estimations in 1973 to be corrected.

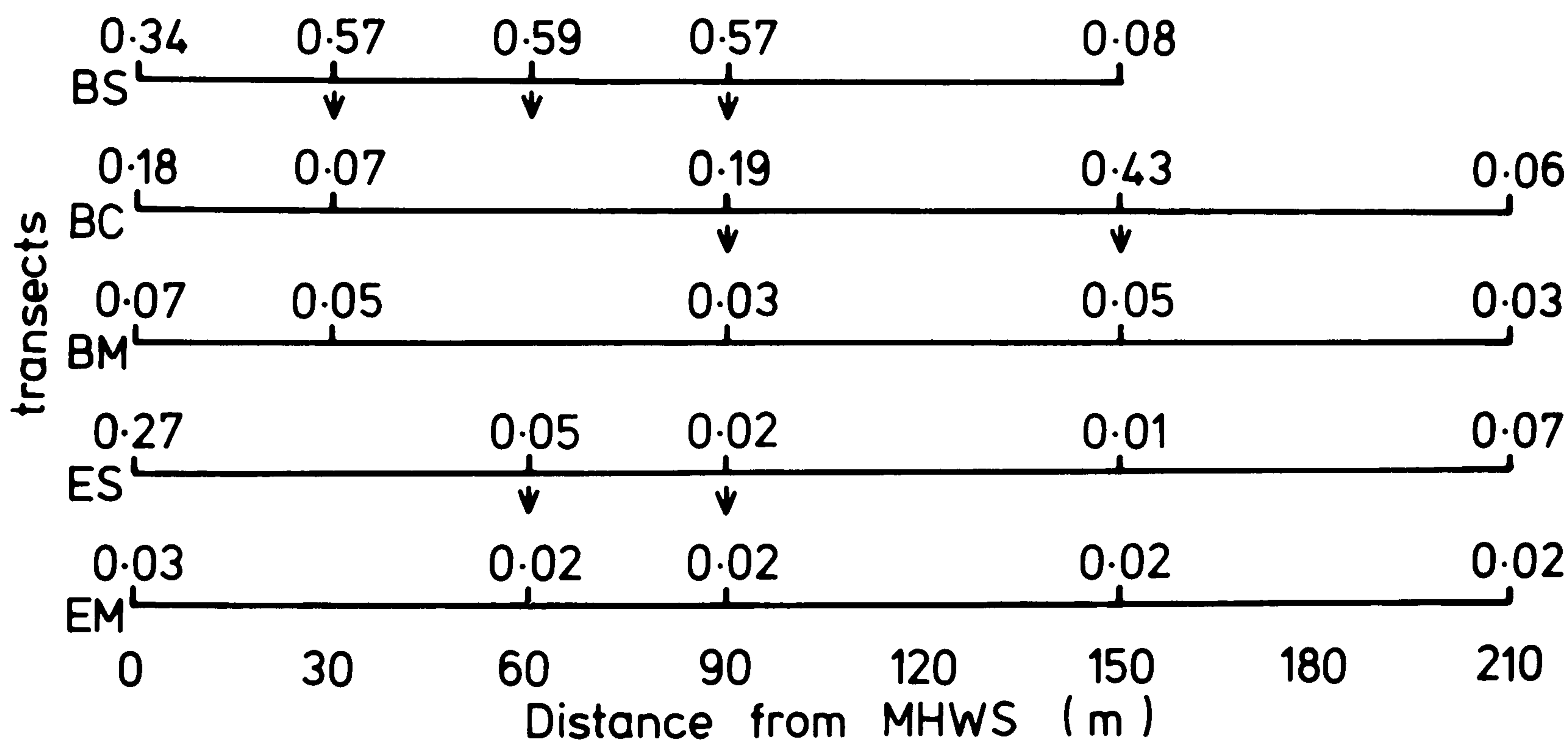
Results (Fig. 9 and Table 4): -

At Site B all samples taken from within areas



t(BM) = 0·512, P>0·1. ∴ no trend. Mean = 0·644
t(EM) = 1·009, P>0·1. ∴ no trend. Mean = 0·286
↓ = sample from within <u>Spartina</u>.

Fig. 9. Carbon content of sediment (%).



t(BM) = 0·559, P>0·1. ∴ no trend. Mean = 0·046
t(EM) = 0·542, P>0·1. ∴ no trend. Mean = 0·022
↓ = sample from within <u>Spartina</u>.

Fig. 10. Nitrogen content of sediment (%).

TABLE 4

Comparison between carbon content values from the three *Spartina* transects (BS, BC and ES) and their appropriate 'baseline' means (from transects BM and EM). Samples from within *Spartina* swards or clumps are indicated thus *.

Sample	*t*	Significance level
BS 0	22.440	0.001
BS 30*	35.730	0.001
BS 60*	39.510	0.001
BS 90*	38.050	0.001
BS 150	2.930	0.05
BC 0	10.180	0.001
BC 30	1.890	ns
BC 90*	12.560	0.001
BC 150*	25.430	0.001
BC 210	0.122	ns
ES 0	53.230	0.001
ES 60*	7.840	0.01
ES 90*	0.100	ns
ES 150	0.220	ns
ES 210	8.160	0.001

ns = not significant

of Spartina growth had significantly greater carbon contents than the baseline mean. Samples BS 0 and BC 0, at the upshore end of the transects, also had significantly greater carbon contents.

At Site E one sample occurring within the Spartina (ES 60) and two at both ends of the transect (ES 0, ES 210) had significantly higher carbon contents than the baseline mean. However, the high value of sample ES 0 may have been due to the presence in the sediment of large amounts of root hair fragments from saltmarsh plants. Similarly, fragments of filamentous algae, noted when collecting sample ES 210, may have been responsible for its high carbon content.

vii. Nitrogen content of sediment.

Between 0.2 g and 0.6 g of ground oven-dried sediment was removed from each of the samples collected for carbon determination (see vi. above) and analysed for nitrogen by the Kjeldahl semi-micro method (Appendix I. p 135). Two estimations were made for each sample and the mean calculated.

Results (Fig. 10 and Table 5): -

At Site B the nitrogen contents of sediments taken from within Spartina clumps or swards (BS 30, BS 60, BS 90, BC 90 and BC 150) were significantly greater than the baseline mean. Samples BS 0 and BC 0 (both at the upshore end of their respective transects) also had significantly higher nitrogen contents than the baseline mean.

At Site E samples ES 60 (Spartina), ES 0, and ES 210 had significantly higher nitrogen contents than the baseline mean (cf. carbon contents). The presence of root hair fragments or filamentous algae in the sediment probably account for two of these

TABLE 5

Comparison between nitrogen content values from the three *Spartina* transects (BS, BC and ES) and their appropriate 'baseline' means (from transects BM and EM). Samples from within *Spartina* swards or clumps are indicated thus *.

Sample	t	Significance level
BS 0	19.820	0.001
BS 30*	35.330	0.001
BS 60*	36.680	0.001
BS 90*	35.330	0.001
BS 150	2.290	ns
BC 0	9.036	0.001
BC 30	1.618	ns
BC 90*	9.710	0.001
BC 150*	25.893	0.001
BC 210	0.944	ns
ES 0	62.000	0.001
ES 60*	7.000	0.01
ES 90*	0.500	ns
ES 150	3.000	0.05
ES 210	12.000	0.001

ns = not significant

findings (ES 0 and ES 210).

viii. Particle size.

Two ~~parameters~~ variables were measured for each site, the percentage formed by the silt/clay fraction, and the median particle diameter. The silt/clay fraction is usually defined as particles less than 62 μ in diameter (Morgans 1956), but in this study was taken as those particles which passed through a 200 mesh per inch sieve ($\simeq$ 125μ)

Approximately 25 g of oven-dried sediment were removed from each of the samples collected for carbon analysis (see vi. above) and the silt/clay fraction estimated as described in Appendix 1, p136. After removal of the silt/clay fraction, the sediment remaining (the sand fraction) was dry sieved for 20 minutes through a graded series of sieves using an Endicott electrical sieve-shaker. The contents of each sieve was then weighed. Samples of sediment retained by each sieve were examined under a 10x binocular microscope and the diameters of at least thirty particles were measured. The mean of the particle sizes so measured for each sieve is given in Table 6. To determine median particle size in an individual sample including the silt/clay fraction, the percentage by dry weight of each particle size was calculated. A graph of percentage cumulative frequency was then plotted for each sample (e.g. BC 0 - Fig. 11). From this the median particle size (i.e. that corresponding to 50% on the ordinate) was obtained.

Results

a. Silt/clay (Fig. 12 & Table 7): -

At Site B all samples on transect BS had a significantly higher silt/clay content than that of the baseline mean. The

TABLE 6

Mean particle size retained by each sieve.

Sieve size (mesh per inch)	Mean size ($\pm$ 2 S.E.s) of particle retained (μ)	
20	1560 $\pm$ 127.4 μ	sand fraction
30	968 $\pm$ 68.6 μ	
40	624 $\pm$ 34.2 μ	
60	429 $\pm$ 30.8 μ	
90	309 $\pm$ 14.4 μ	
120	226 $\pm$ 15.7 μ	
200	178 $\pm$ 16.3 μ	
sub-sieve	126 $\pm$ 8.2 μ	silt/clay fraction

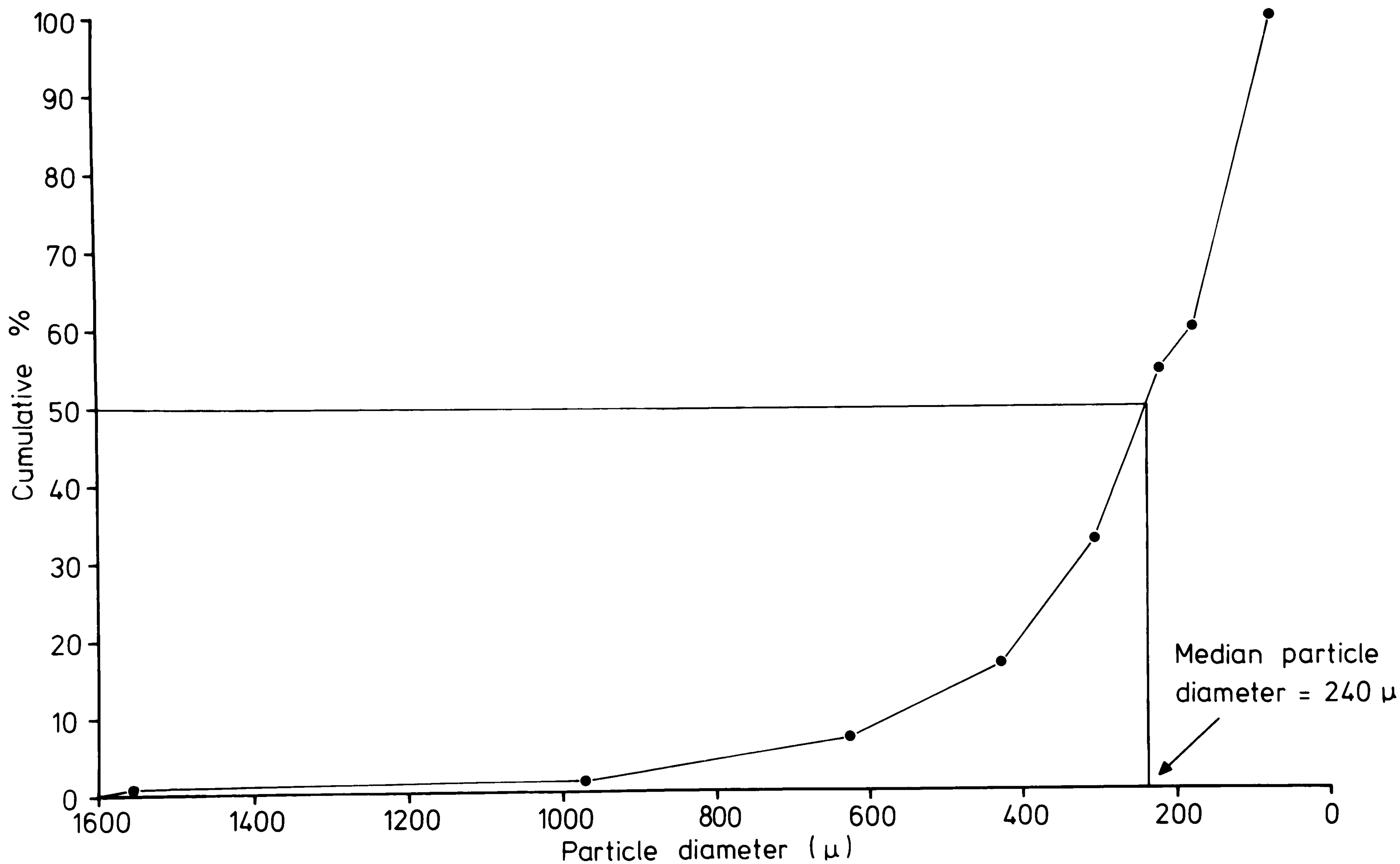
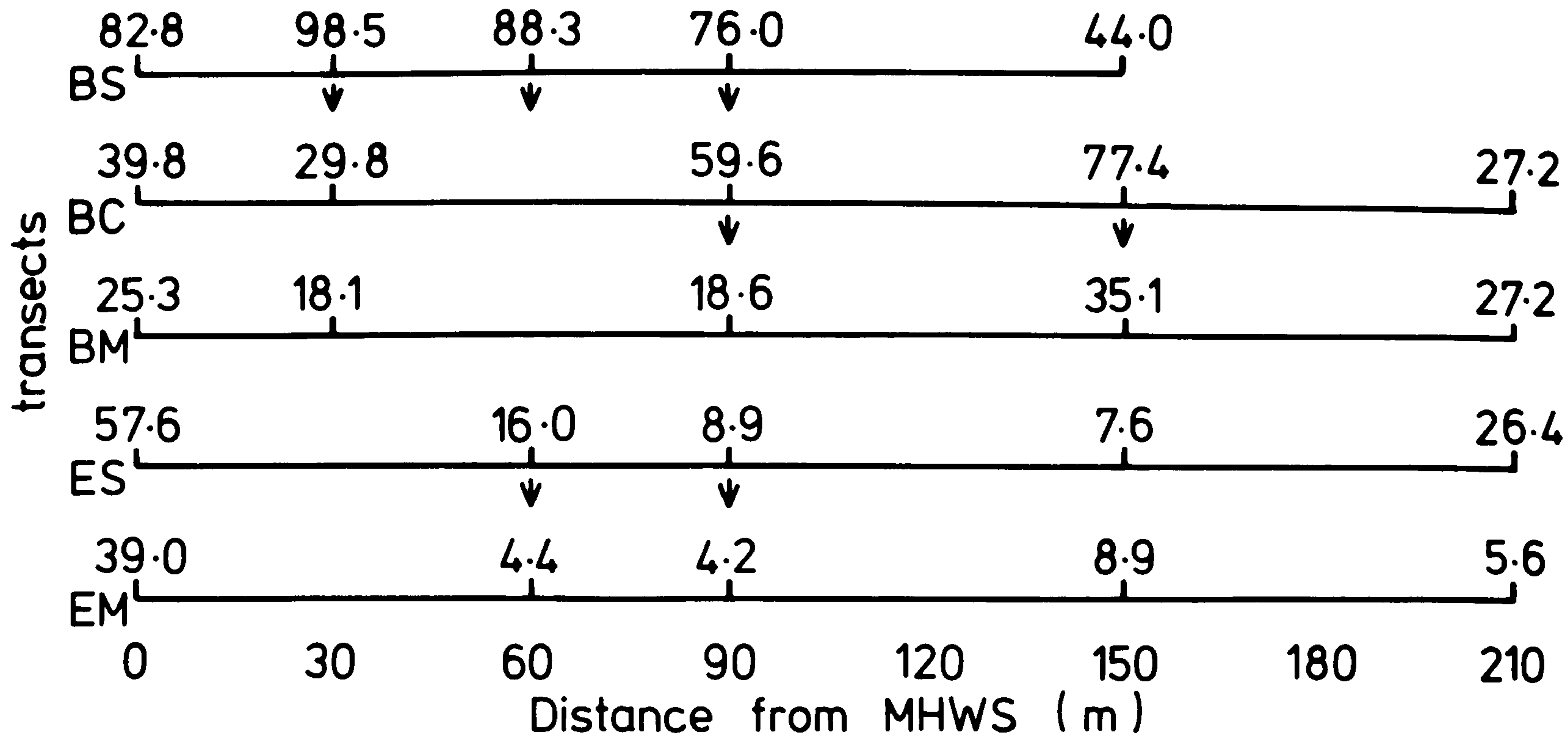


Fig. 11. Cumulative frequency graph for sample BC 0.

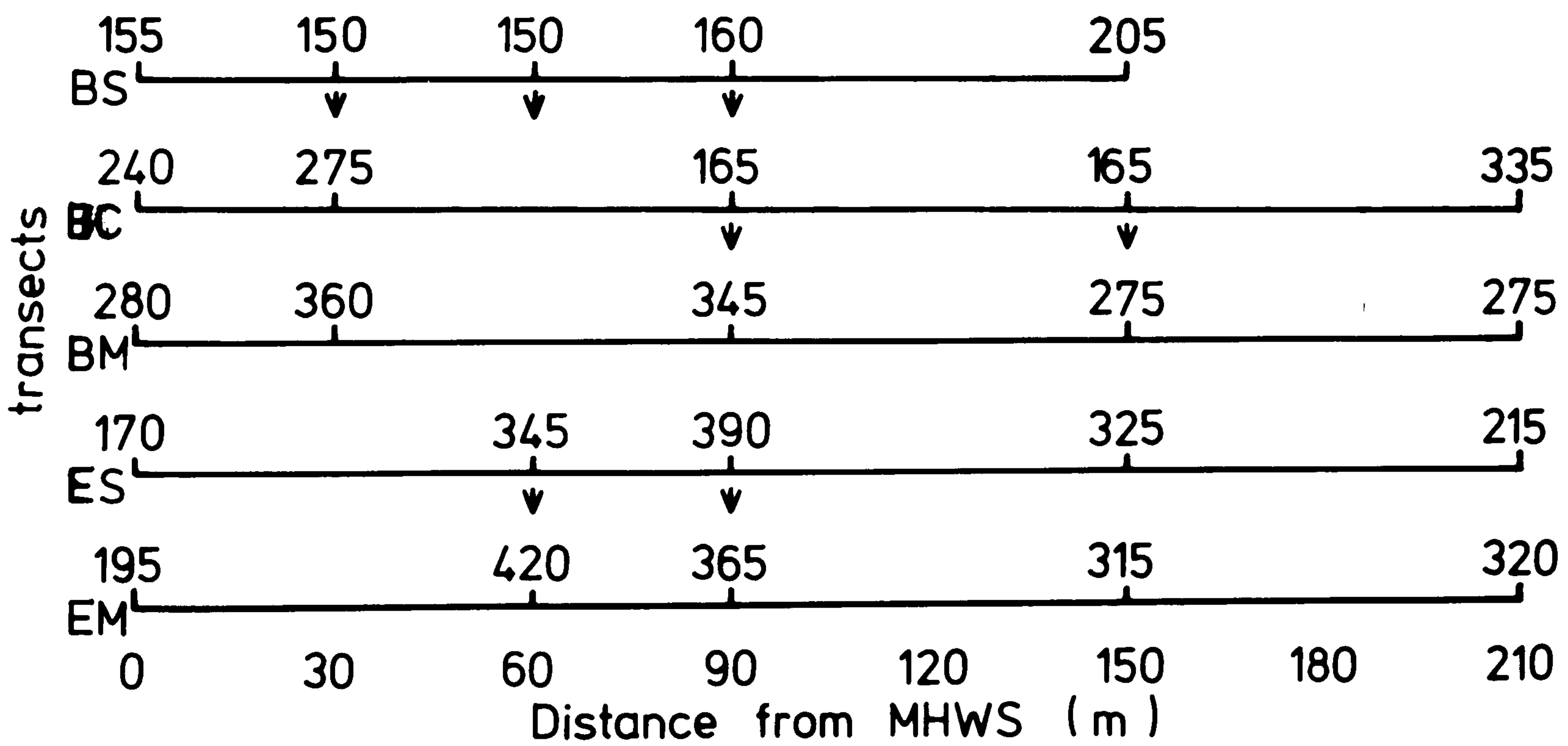


t (BM) = 1·063, P>0·1. ∴ no trend. Mean = 24·9

t (EM) = 1·503, P>0·1. ∴ no trend. Mean = 12·4

↓ = sample from within _Spartina_.

Fig. 12. Silt/clay content of sediment (%).



↓ = sample from within _Spartina_.

Fig. 13. Median particle diameter (μ).

TABLE 7

Comparison between silt/clay content values from the three *Spartina* transects (BS, BC and ES) and their appropriate 'baseline' means (from transects BM and EM). Samples from within *Spartina* swards or clumps are indicated thus *.

Sample	*t*	Significance level
BS 0	9.275	0.001
BS 30*	11.790	0.001
BS 60*	10.150	0.001
BS 90*	8.180	0.01
BS 150	3.060	0.05
BC 0	2.390	ns
BC 30	0.794	ns
BC 90*	5.558	0.01
BC 150*	8.412	0.01
BC 210	0.375	ns
ES 0	3.366	0.05
ES 60*	0.266	ns
ES 90*	0.263	ns
ES 150	0.364	ns
ES 210	1.045	ns

ns = not significant

two highest values occurred within the *Spartina* sward. Transect BC gave similar results with significantly higher silt/clay contents occurring within the *Spartina*.

At Site E only sample ES 0 had a significantly higher silt/clay content than the baseline mean. Further significant differences may have emerged if the high silt/clay content of sample EM 0 had been ignored when calculating the baseline mean. It seems likely that the high value obtained for this sample was due to accretion of silt/clay particles by the root network of the saltmarsh plants growing there.

b. Median particle diameter (Fig. 13).

Since median values were calculated, parametric statistics could not be used for comparison. At Site B all samples within *Spartina* were compared with their respective samples outside at equivalent tidal levels (Table 8). The median particle diameter within *Spartina* was found to be significantly lower than that outside at equivalent tidal levels.

At Site E only one of the two *Spartina* samples had a lower median particle diameter than the corresponding sample outside *Spartina*.

ix. Correlation of silt/clay content with carbon and nitrogen content, and depth of redox-potential-discontinuity.

Silt/clay contents were plotted against carbon content (Figs. 14 and 15), nitrogen content (Figs. 16 and 17), and depth of R.P.D. (Figs. 18 and 19) for both Sites B and E. Correlation coefficients were also calculated.

All correlations were significant except that for silt/clay content against depth of R.P.D. at Site E. Strong positive

TABLE 8

Comparison between median particle diameter values from *Spartina* and non-*Spartina* samples at equivalent tidal levels at Site B. Samples with the lower median particle diameter of the pair are indicated thus *.

Spartina sample	non-*Spartina* sample
BS 30*	BC 30
BS 30*	BM 30
BS 90*	BM 90
BC 90*	BM 90
BC 150*	BS 150
BC 150*	BM 150

Probability that *Spartina* samples have a lower median particle diameter than non-*Spartina* samples $= (\frac{1}{2})^6$

$= 0.012\ (< 0.05)$

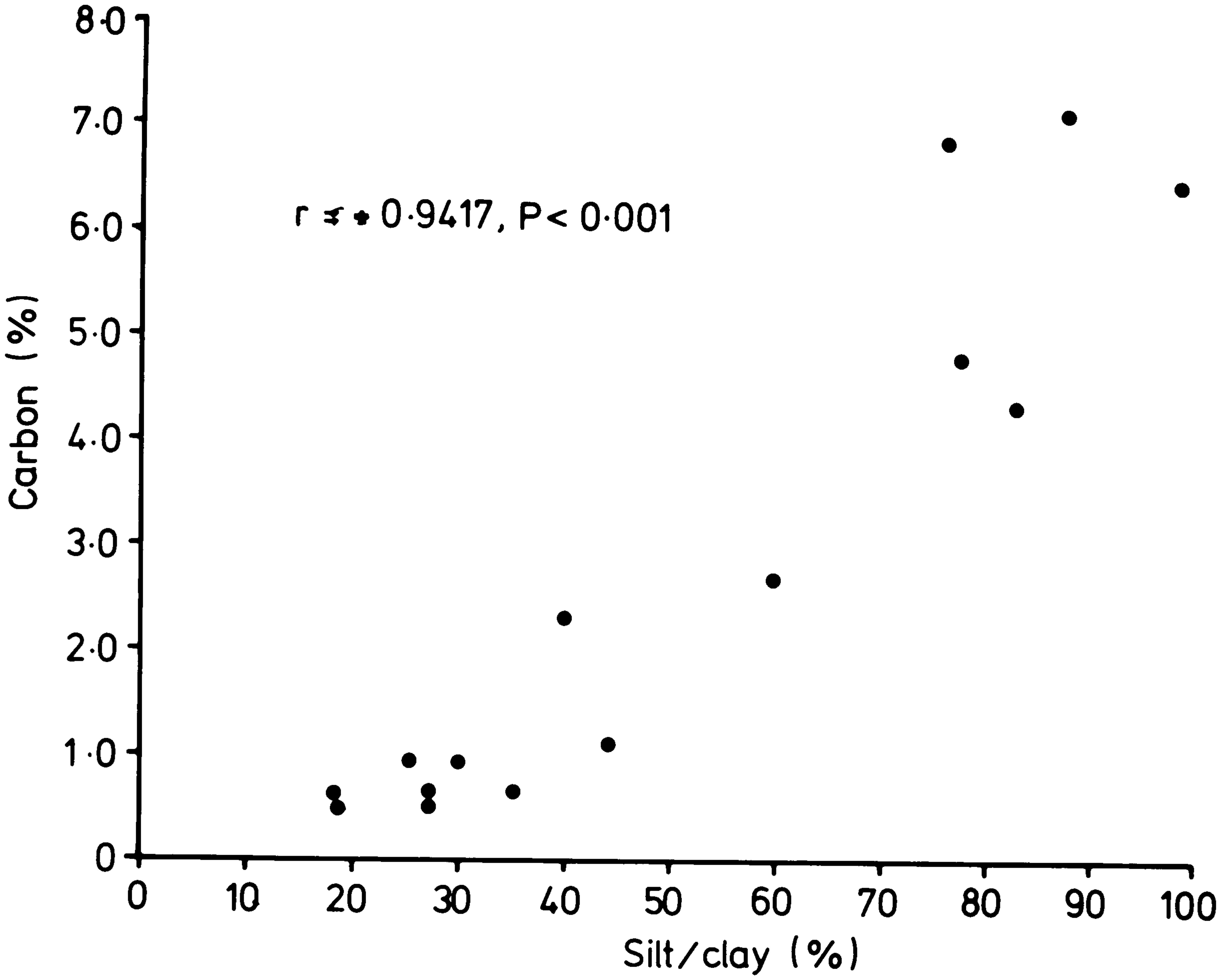


Fig.14. The carbon content of sediment related to silt/clay content at Site B.

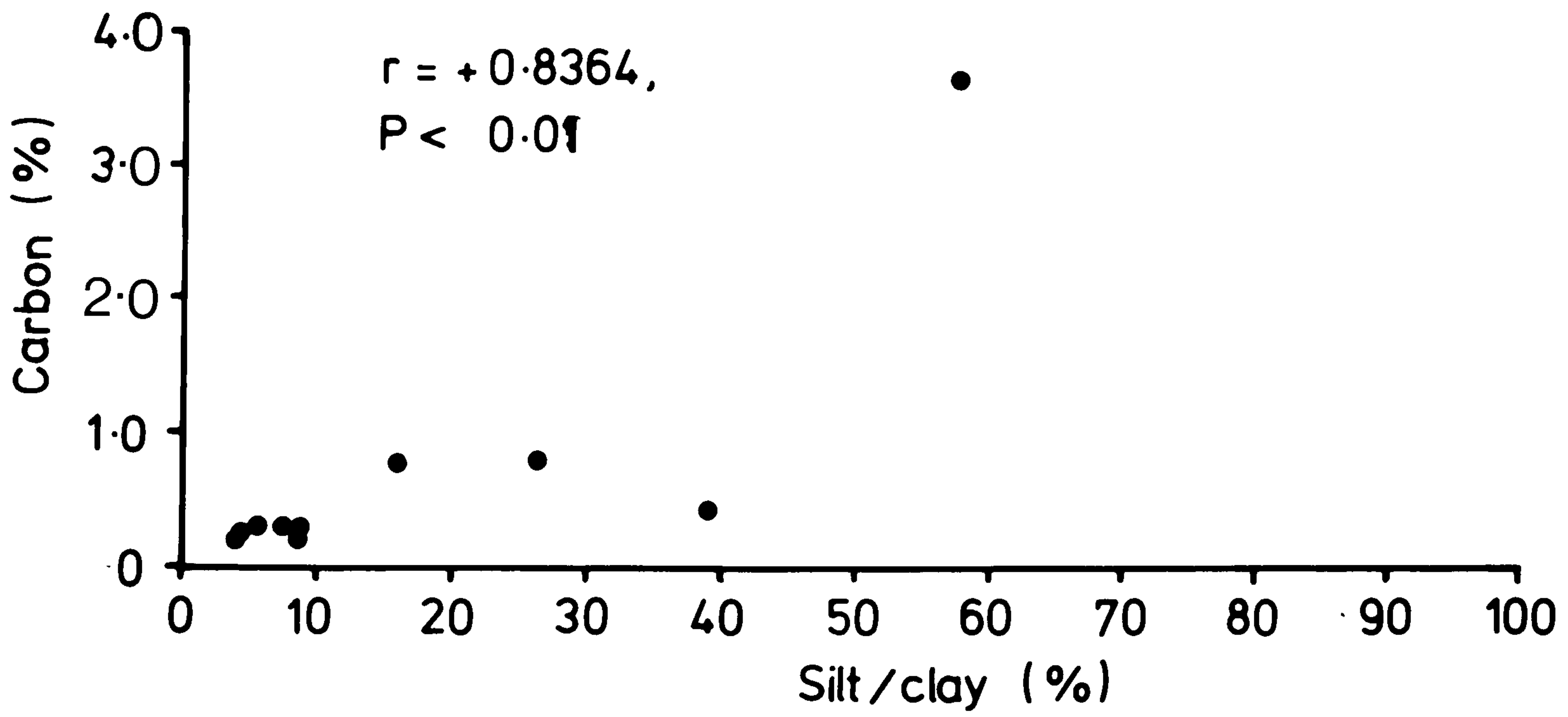


Fig. 15. The carbon content of sediment related to silt/clay content at Site E.

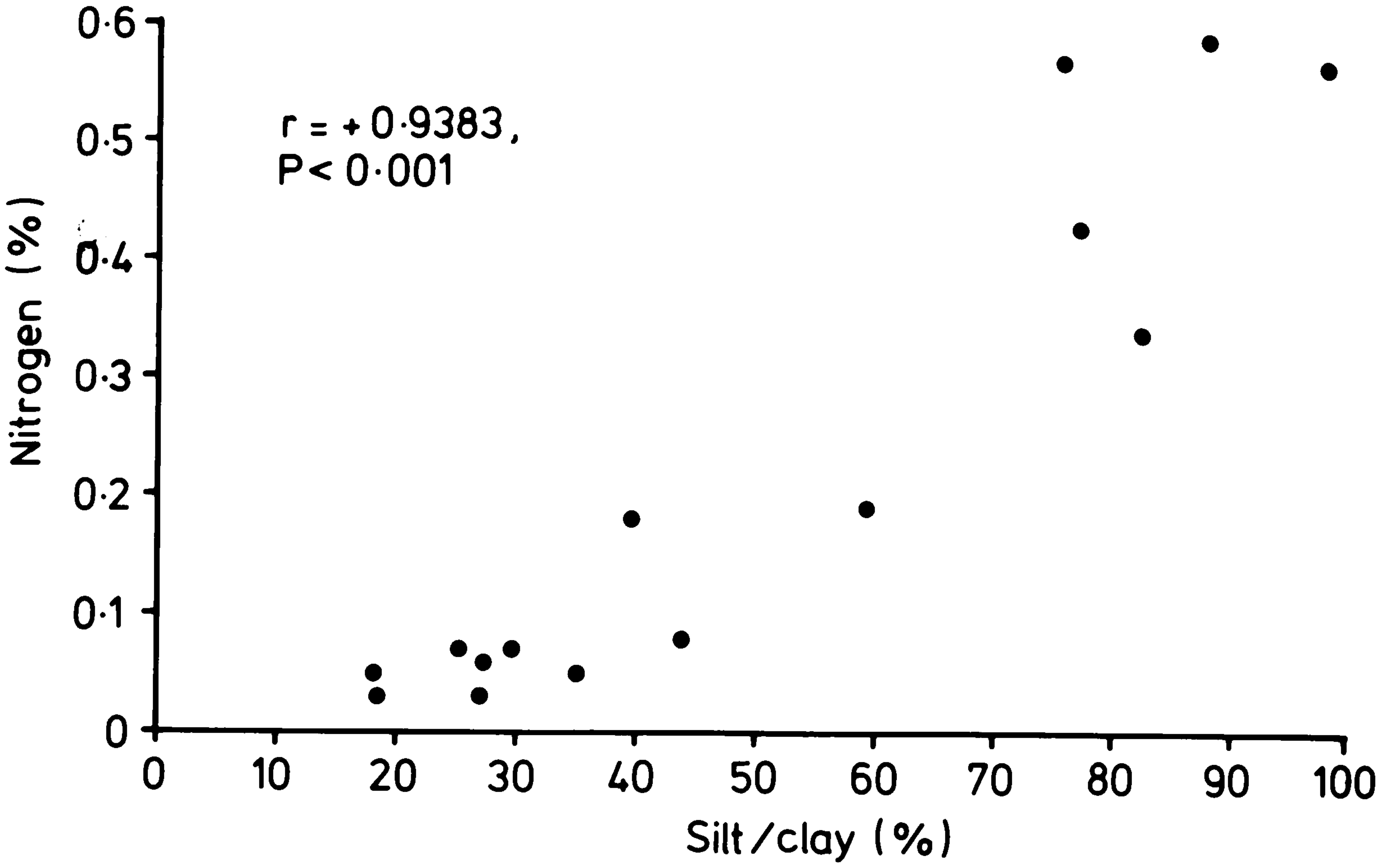


Fig. 16. The nitrogen content of sediment related to silt/clay content at Site B.

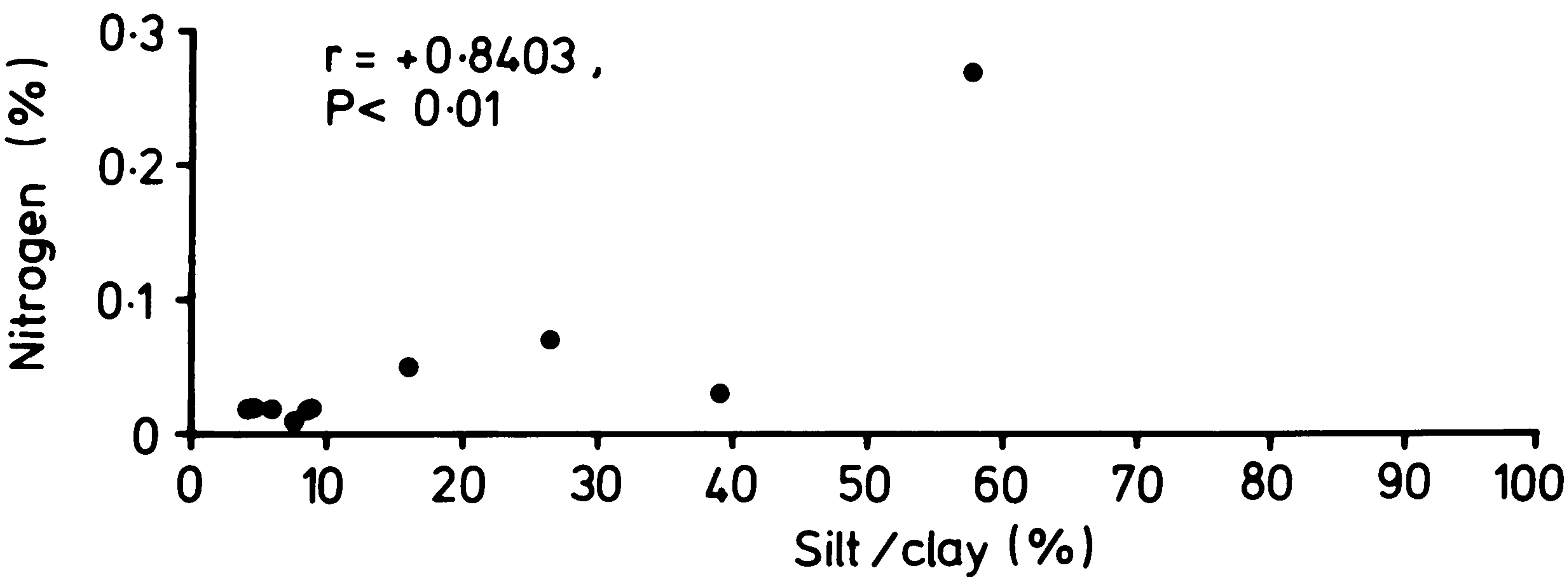


Fig. 17. The nitrogen content of sediment related to silt/clay content at Site E.

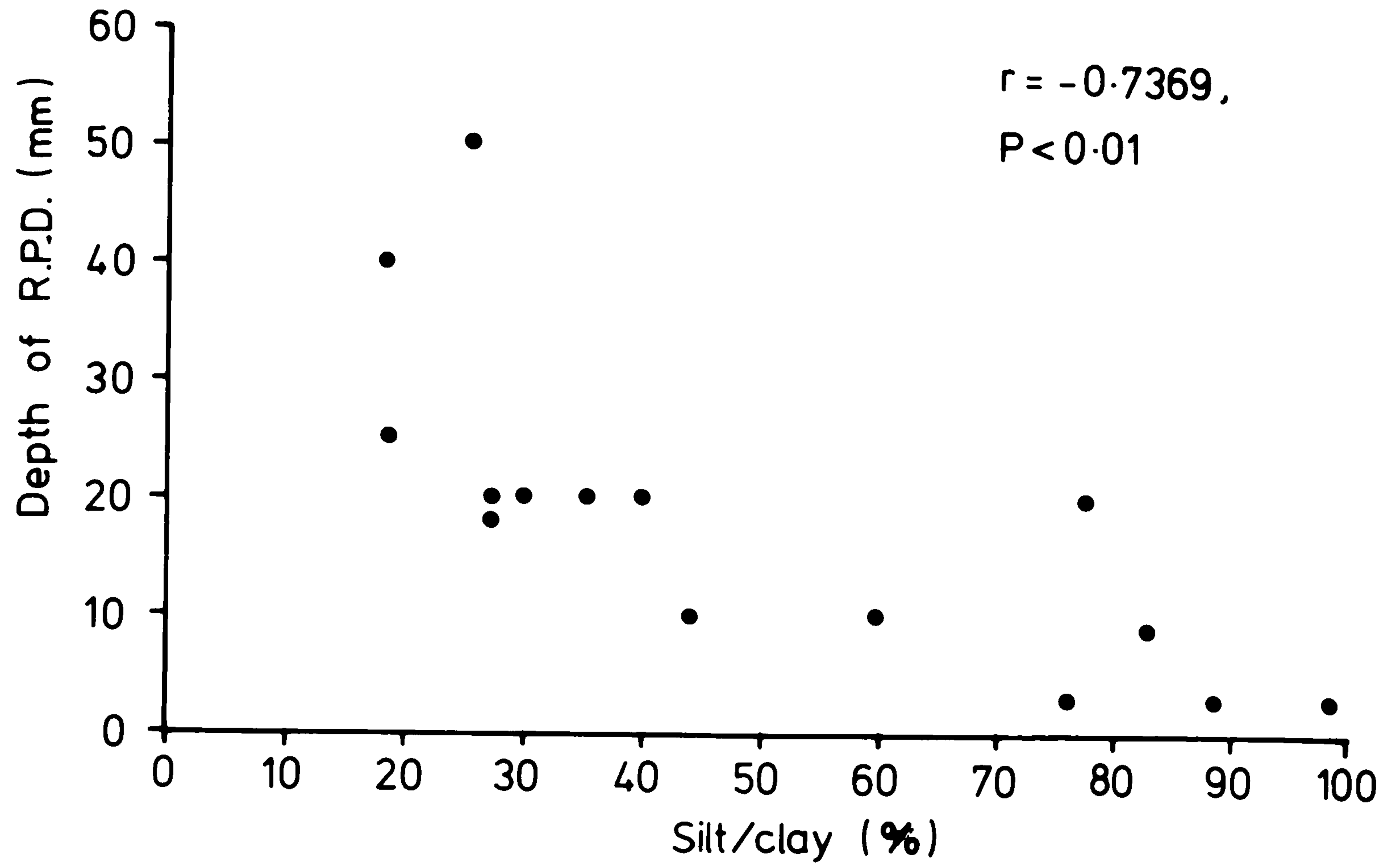


Fig. 18. The depth of the redox-potential-discontinuity related to silt/clay content at Site B.

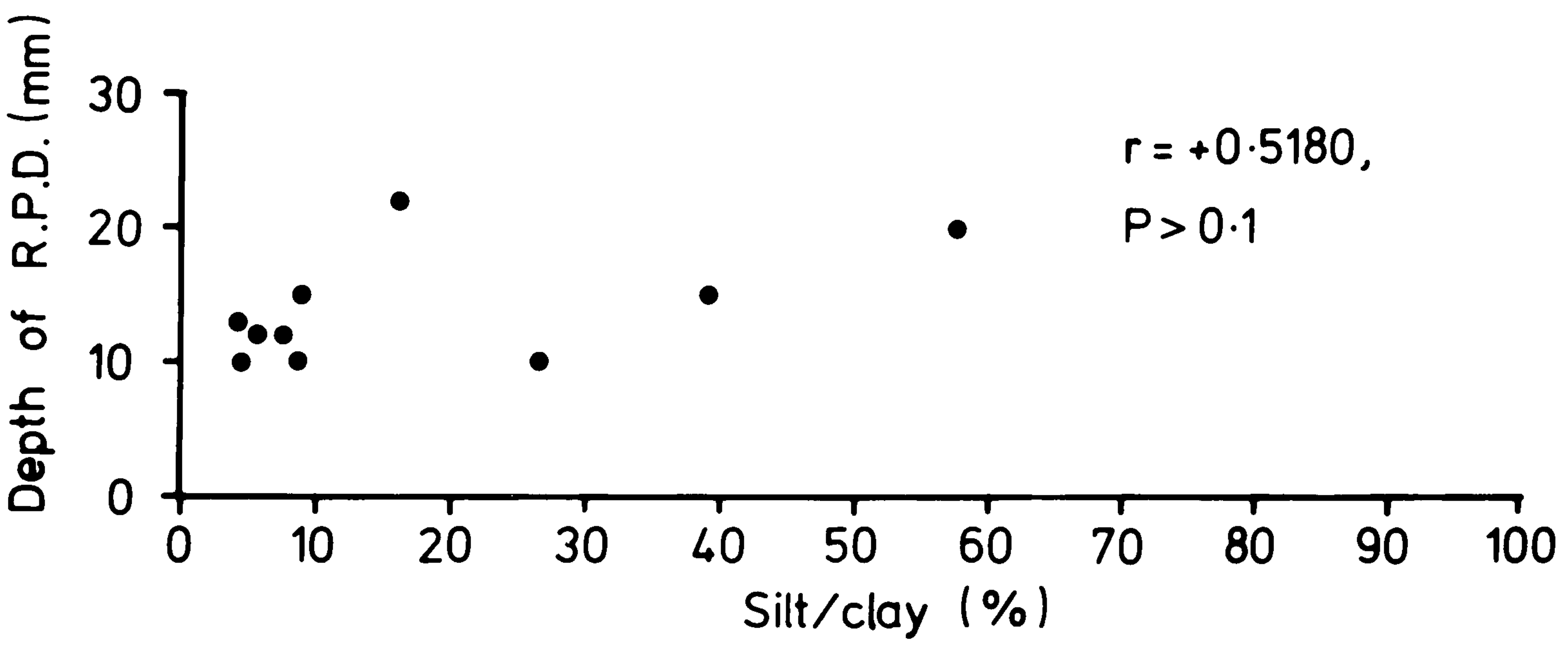


Fig. 19. The depth of the redox-potential-discontinuity related to silt/clay content at Site E.

correlations between silt/clay and both carbon and nitrogen contents were also found by Newell (1965) and indicate a close relationship between the silt/clay content of the sediment and the potential food available to deposit feeders. Shallow depths of R.P.D. at Site B were clearly related to high silt/clay contents, as stated by Fenchel and Riedl (1970). The inconclusive result for Site E (Fig. 19) suggests that other factors (e.g. freshwater seepage) were predominant in determining the depth of R.P.D.

x. Sediment characteristics of *Spartina* marsh - Summary.

Negligible differences were found between the salinity of interstitial water inside and outside *Spartina* at either site.

At Site B (Budle Bay) sediment from *Spartina* marsh had higher silt/clay, carbon, nitrogen and interstitial water contents than that outside *Spartina*. In addition, the median particle diameter was smaller than outside *Spartina* and the R.P.D. was nearer the surface.

At Site E (Elwick-Cockly Knowes) no consistent differences between sediment characteristics inside and outside *Spartina* were found. This probably followed from the similarity in particle size inside and outside the *Spartina*, since most other sediment characteristics were strongly correlated with particle size.

CHAPTER 4. DENSITIES OF INVERTEBRATE SPECIES IN SPARTINA MARSHES

i. Sample collection and extraction

Mud samples measuring 10 cm x 10 cm in area and up to 25 cm in depth were collected using the metal sampler illustrated in Fig. 20a. If required, the sample was divided into two or more layers by sliding a metal plate between two corresponding slits as illustrated (Fig. 20b). Samples were taken to the laboratory in labelled polythene bags.

In the laboratory, invertebrates were extracted immediately, or if this was impossible, samples were stored in the 10°C constant temperature room. For extraction, each sample was washed through a 20 or 30 mesh per inch sieve using a flexible hose attached to a tap. In this way sufficient directed pressure was obtained to remove quickly most of the sand and silt. When sieving was complete, the residue was transferred to an enamel dish containing filtered seawater where the animals were removed by systematic sorting of the debris. The use of seawater as a medium for sorting ensured that live molluscs became active again and could be distinguished easily from dead or empty shells. The animals in each sample were identified and counted. Specimens were then preserved in 10% formalin or deep frozen for dry weight determination.

ii. Sampling programme

The number of samples which can be handled during any sampling programme is limited by time and apparatus. It is therefore important that the location of each sampling site is selected carefully to maximise the information made available by the programme. To determine

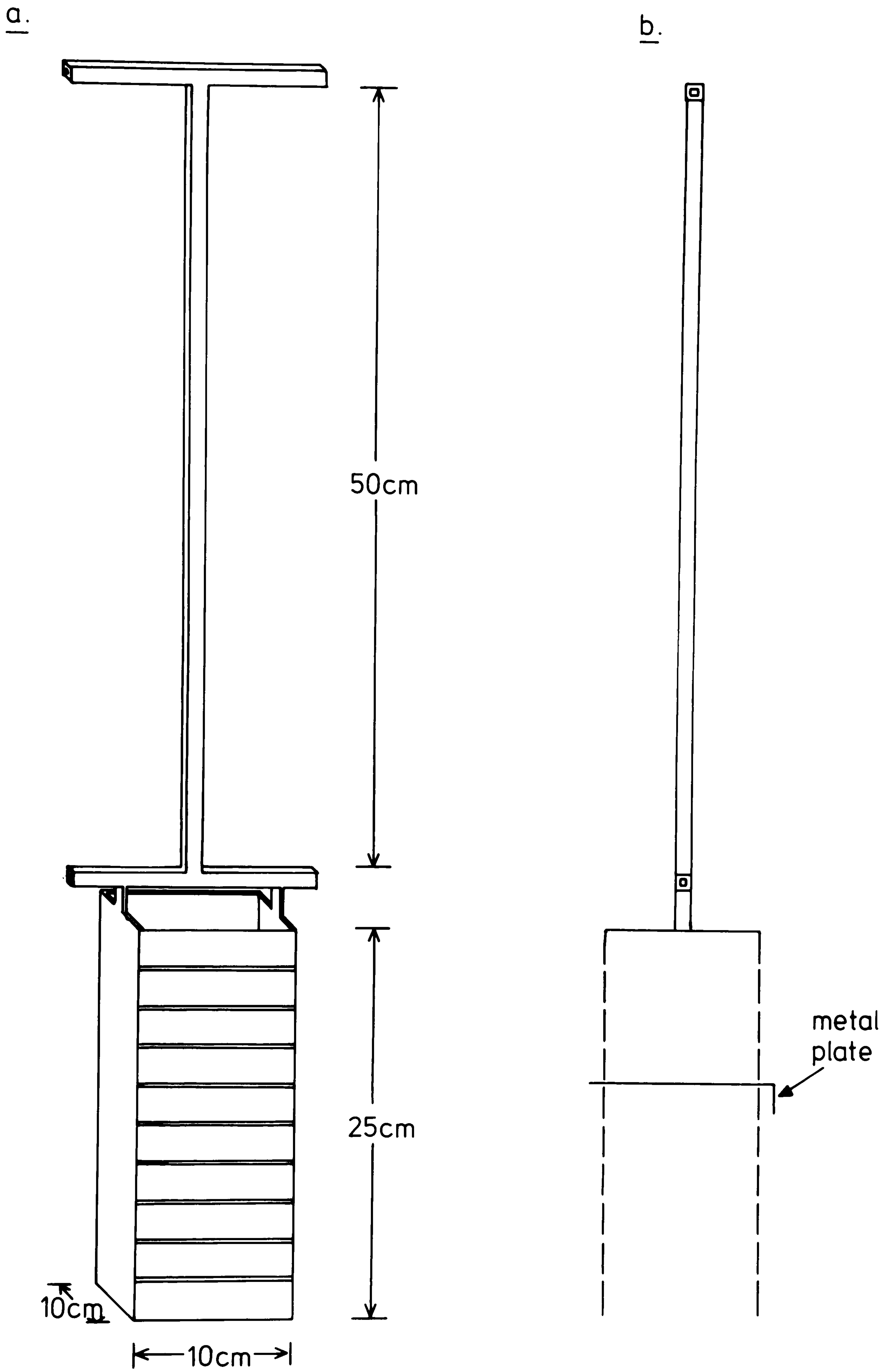


Fig. 20. Mud sampler.

major differences between invertebrate populations inside and outside areas of Spartina, samples were taken along transects running downshore from MHWS in each of three habitats (Spartina swards, Spartina clumps and open mud). This method of sampling takes account of any zonation of species within each habitat but ignores possible alongshore variations, due, for example, to areas of freshwater seepage, which might affect the invertebrate species present. In addition, results from individual stations along a single transect may be affected by marked variations in invertebrate density over a very small area (e.g. 1 m^2). This local variation is often as great as, or greater than, variation between average densities much further apart (e.g. 100 m). Therefore, the importance of these two possible sources of variation was investigated in certain common invertebrate species before the main sampling programme was undertaken.

a. Alongshore variation.

An area at Elwick (Site W) was selected where four species relevant to the study were known to occur (Nereis diversicolor, Hydrobia ulvae, Corophium volutator and Scoloplos armiger). Four parallel transects separated by 20 m intervals were staked out from MHWS downshore for 180 m (Fig. 4). For the first 75 m, the transect lay through a Spartina sward inhabited by Nereis; the remaining 105 m crossed open mud inhabited by Hydrobia and Scoloplos. Samples were collected at stations along the transect and sieved through 20 and 30 mesh per inch sieves. The results are given in Table 9.

Two-way analyses of variance were performed on each of the four species to determine the amount of between-transect variation and between-tidal-level variation (Table 10). The two sections of each

TABLE 9

Numbers of each species from the study of alongshore variation of invertebrates at Site W.

Distance from MHWS (m)	*Hydrobia ulvae*				*Scoloplos armiger*			
TRANSECT	i	ii	iii	iv	i	ii	iii	iv
180	14	24	16	5	14	8	12	14
160	13	43	15	9	10	24	7	10
140	11	11	5	2	10	13	7	27
120	7	1	1	-	5	-	-	-
100	-	-	4	2	23	4	2	7
	Nereis diversicolor				*Corophium volutator*			
75	2	3	4	4	-	-	-	-
65	7	7	-	8	-	-	-	-
45	3	2	-	2	-	-	-	-
32	10	3	1	6	7	-	-	-
22	5	3	10	7	-	-	3	-
17	4	-	7	3	25	-	1	-
15	-	2	2	5	-	4	7	23

TABLE 10

Analyses of variance for each species from the study of alongshore variation of invertebrates at Site W.

	Source of variation	Degrees of freedom	Corrected sum of squares	Mean Square	F Value	P
Hydrobia ulvae	Between transects	3	379.75	126.58	2.413	>0.1
	Between tidal levels	4	1035.30	258.83	4.934	<0.05
	Residual	12	629.50	52.46		
	Total	19	2044.55			
Scoloplos armiger	Between transects	3	138.15	46.05	0.940	>0.25
	Between tidal levels	4	428.30	107.08	2.185	>0.1
	Residual	12	588.10	49.01		
	Total	19	1154.55			
Nereis diversicolor	Between transects	3	19.57	6.52	0.935	>0.25
	Between tidal levels	6	68.86	11.48	1.645	>0.1
	Residual	18	139.43	6.97		
	Total	27	227.86			
Corophium volutator	Between transects	3	66.43	22.14	0.539	>0.25
	Between tidal levels	6	297.50	49.58	1.208	>0.25
	Residual	18	739.07	41.06		
	Total	27	1103.00			

transect were treated separately for this analysis.

No significant differences were found between transects in the densities of any of the four species studied; i.e. alongshore variation was insignificant in a distance of 60 m. Hydrobia was the only species with significantly different mean densities between tidal levels. In view of the lack of alongshore variation, one transect in each habitat was considered sufficient to compare the invertebrate populations of the three habitats; i.e. continuous Spartina sward, Spartina clumps and open mud.

b. Local variations in density.

Variations within a small area are detected efficiently only by sampling the whole of that area. Variation between pairs of adjacent samples can then be compared with variation between pairs of randomly selected samples within the whole area. In this study, comparisons were made (1) by collecting a block of 16 adjacent samples and (2) by taking paired samples along a transect to investigate the effect over a much larger area.

(1) Block sampling: - An area of open mud at Teal Hole (Fig. 1), 70 m downshore from MHWS, was selected for its abundant Corophium and Nereis populations. A block of mud 40 cm x 40 cm was removed in the form of 16 separate 10 cm x 10 cm samples, each taken to a depth of 25 cm. The animals were extracted by sieving. Results are given in Table 11. The mean of the variations in numbers of animals in 24 pairs of adjacent samples was then compared with the mean of the variations in 24 pairs of randomly selected samples (Table 12). No significant difference was found between either of these two means in the 40 cm x 40 cm sampling area.

TABLE 11

Numbers of Corophium volutator (C) and Nereis diversicolor (N) from the block sampling to study possible variation in densities due to local clumping. The variation between each pair of squares was calculated by subtracting the smaller number of animals from the larger (e.g. variation in Corophium numbers between samples 1a. and 1b. is 42 minus 25, i.e. 17).

	1	2	3	4
a	N 7 C 42	N 5 C 43	N 5 C 44	N 11 C 35
b	N 7 C 25	N 7 C 42	N 6 C 45	N 11 C 44
c	N 5 C 26	N 5 C 28	N 8 C 37	N 8 C 29
d	N 6 C 27	N 4 C 38	N 6 C 22	N 3 C 49

TABLE 12

Comparison between the means of the variation in numbers of invertebrates (*Corophium volutator* and *Nereis diversicolor*) in 24 pairs of adjacent samples and in 24 pairs of randomly selected samples. Sampling was carried out in a block of 16 samples at Teal Hole.

	Mean variation between 24 pairs of adjacent samples	Mean variation between 24 pairs of randomly selected samples	t	p
Corophium volutator	8.63 $\pm$ 2.86	10.34 $\pm$ 2.50	0.899	>0.1
Nereis diversicolor	1.88 $\pm$ 0.86	2.08 $\pm$ 0.81	0.354	>0.1

(2) Transect sampling: - At Site W a transect (v.) was staked out from MHWS downshore through <u>Spartina</u> for 80 m (Fig. 4). Paired adjacent 10 cm x 10 cm samples were collected to a depth of 25 cm at each of 7 stations along the transect and variations in numbers of <u>Nereis</u> were compared as described above for block sampling. Results are given in Table 13. No significant difference was found ($t = 0.624$, $P > 0.1$) between the mean of the variations in numbers of <u>Nereis</u> between paired adjacent samples (4 ± 1.95) and the mean of the variations in numbers between randomly paired samples (5 ± 2.54).

Results from the Block Sampling and the Transect Sampling both indicated that variation between adjacent samples was almost as great as (and not significantly different from) that between samples further apart. It was therefore decided to take single samples from many stations, rather than several samples at a few stations, along a transect during the summer programme. This established the possible zonation of each species. During the following winter one sample was taken from each of the four corners of a square metre at each sampling station. This higher intensity of sampling at fewer stations was undertaken to determine how definitive the summer zonations were. Results from individual samples collected in the winter programme are given in Appendix 2, p137.

iii. <u>General invertebrate survey</u>

Measurements of invertebrate population densities were made in the two main study Sites B and E, (Figs. 2 and 3) in both summer and winter, to determine possible seasonal changes. Less detailed measurements of invertebrate densities were made in two other areas where <u>Spartina</u> occurred (Fenham Mill, Fig. 1, and Site W, Fig. 4) to

TABLE 13

Numbers of *Nereis diversicolor* from the transect sampling to study possible variation in densities due to local clumping.

	Distance from MHWS (m)						
	15	20	25	35	45	55	65
Adjacent pairs of samples	-	8	8	10	5	5	12
	-	11	5	4	10	2	4

establish how far results from the main study areas held generally.

a. Site B.

Samples were collected in June and December of 1973.

Corophium volutator (Fig. 21): -

In June Corophium was scarce within the Spartina sward (transect BS) and clumps (transect BC), but present in large, albeit variable, numbers in the open mud. By December there were increased densities at the upshore end of all three transects, particularly BC. Beyond 150 m from MHWS Corophium was absent from the whole area.

Hydrobia ulvae (Fig. 22): -

In June, Hydrobia was present in densities of up to 4000 per m^2 on the Spartina clump and open mud transects. However, densities in the first 60 m of the Spartina sward were very small, increasing noticeably only at 90 m from MHWS. The December distribution was similar to that in June, with low densities in the first 30 m of transects BC and BM and the first 60 m of transect BS. In addition, overall densities both in transects BS and BC were smaller in December than in June.

Macoma balthica (Fig. 23a): -

Macoma was totally absent within the Spartina sward in both June and December and within the Spartina clumps in June. By December, however, there were small numbers present within a clump 150 m from MHWS. In the open mud Macoma was present at slightly lower densities in December than June.

Arenicola marina (Fig. 23b): -

Arenicola was absent from the sward and the Spartina clumps during both June and December. The density in open mud

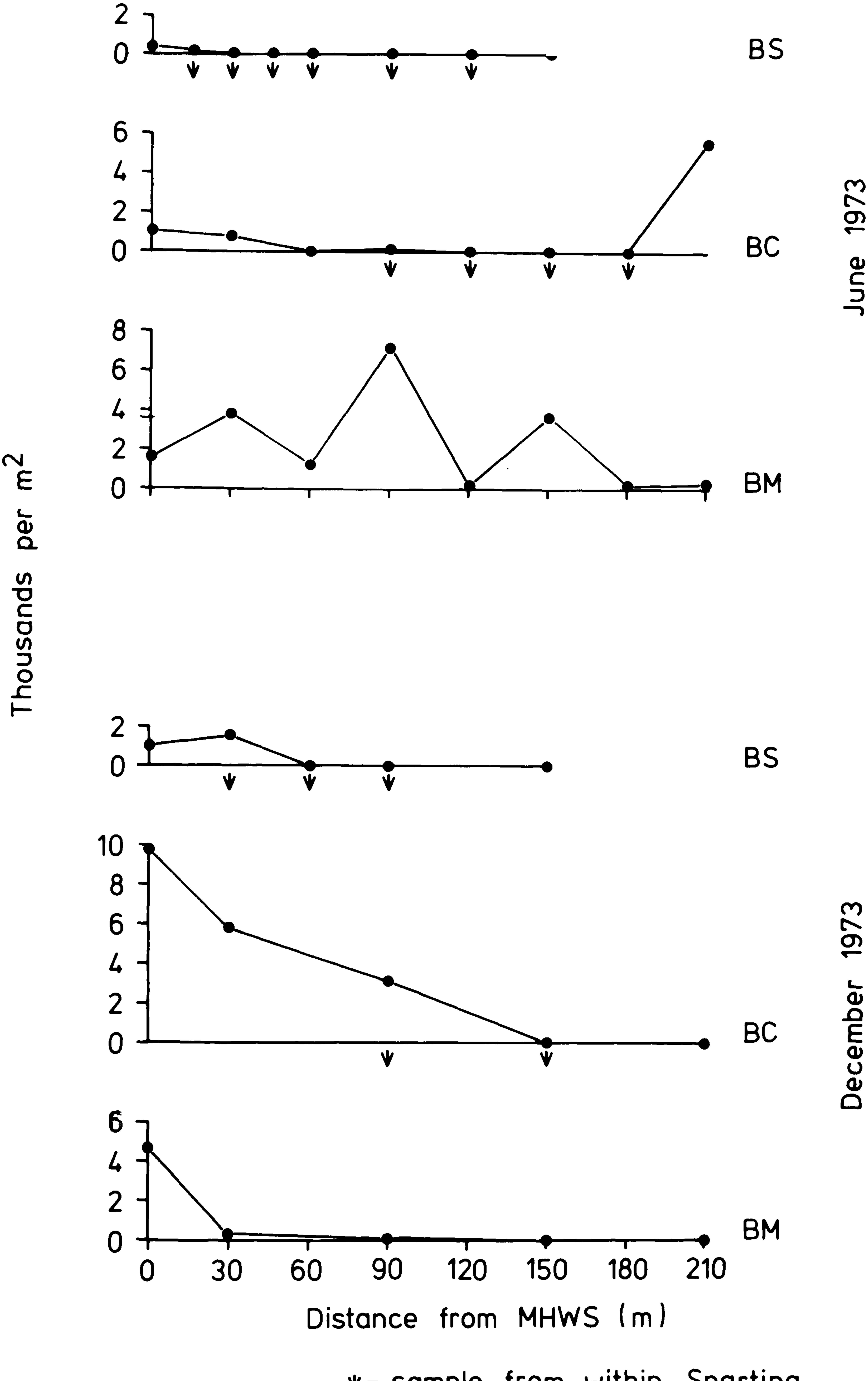


Fig. 21. Density of *Corophium volutator* at Site B.

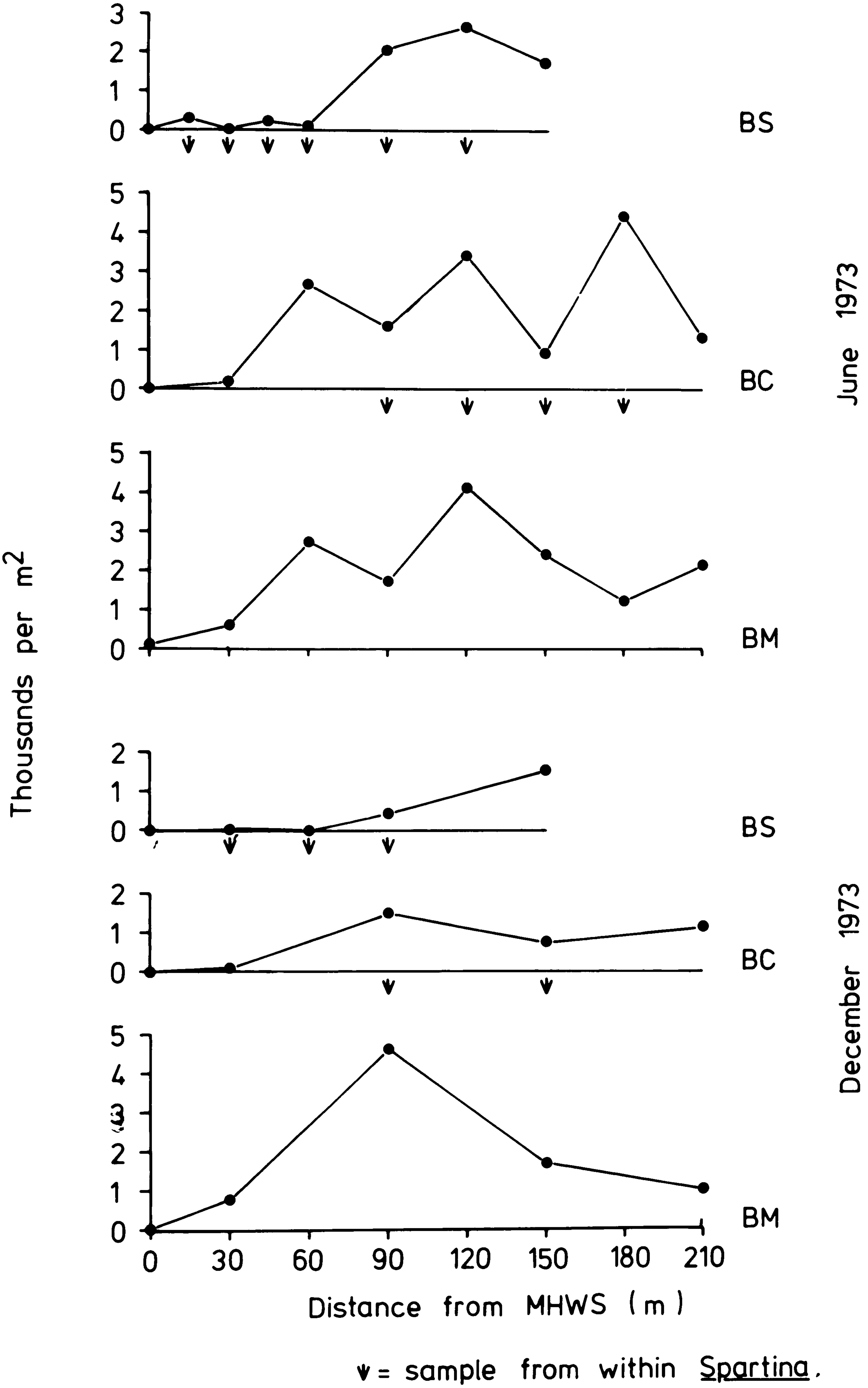


Fig. 22. Density of Hydrobia ulvae at Site B.

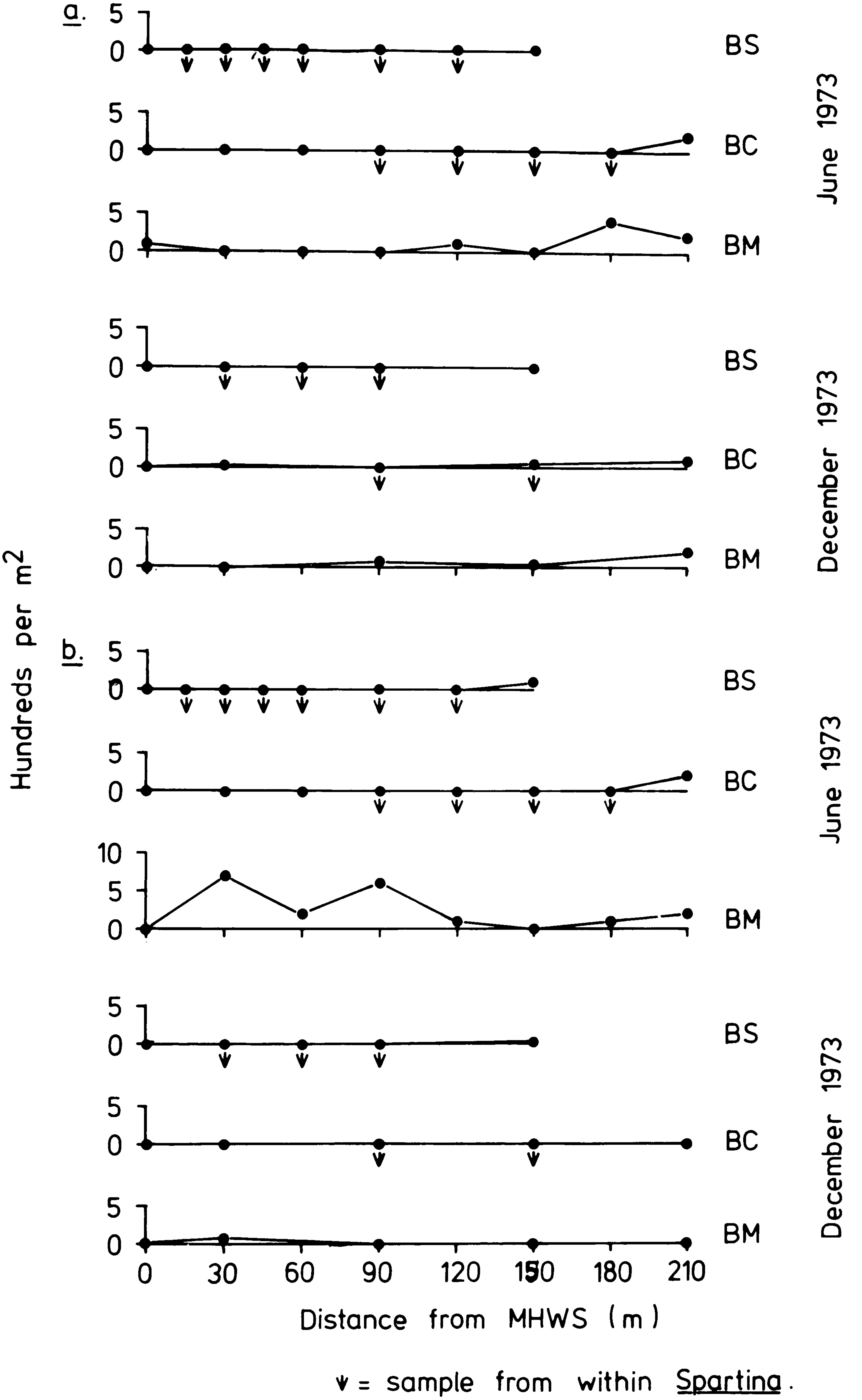


Fig. 23. Density of a. *Macoma balthica* and b. *Arenicola marina* at Site B.

was considerably lower in December than in June.

Nereis diversicolor (Fig. 24a): -

Nereis was absent from within the Spartina sward and clumps during June and from within the sward during December.

Carcinus maenas (Fig. 24b): -

Carcinus was present within both Spartina transects but totally absent from the open mud during both June and December.

Scoloplos armiger (Fig. 25a): -

Scoloplos was restricted to the open mud, apart from the sample BS 90 within the Spartina sward in June. There was a noticeable increase in density and range in the open mud between the June and December samplings.

Littorina "saxatilis" (Fig. 25b): -

This "species" was present within the Spartina sward and clumps during both June and December. It was also present on the open mud in relatively small numbers during December. No attempt was made to differentiate the various forms, which have now been described as four distinct sympatric species (Heller 1975).

b. Site E.

Samples were collected in August and December 1973.

Hydrobia ulvae (Fig. 26a): -

In both August and December considerably larger densities of Hydrobia were present on the Spartina transects than in the open mud. In December the largest densities of Hydrobia were found within clumps of Spartina.

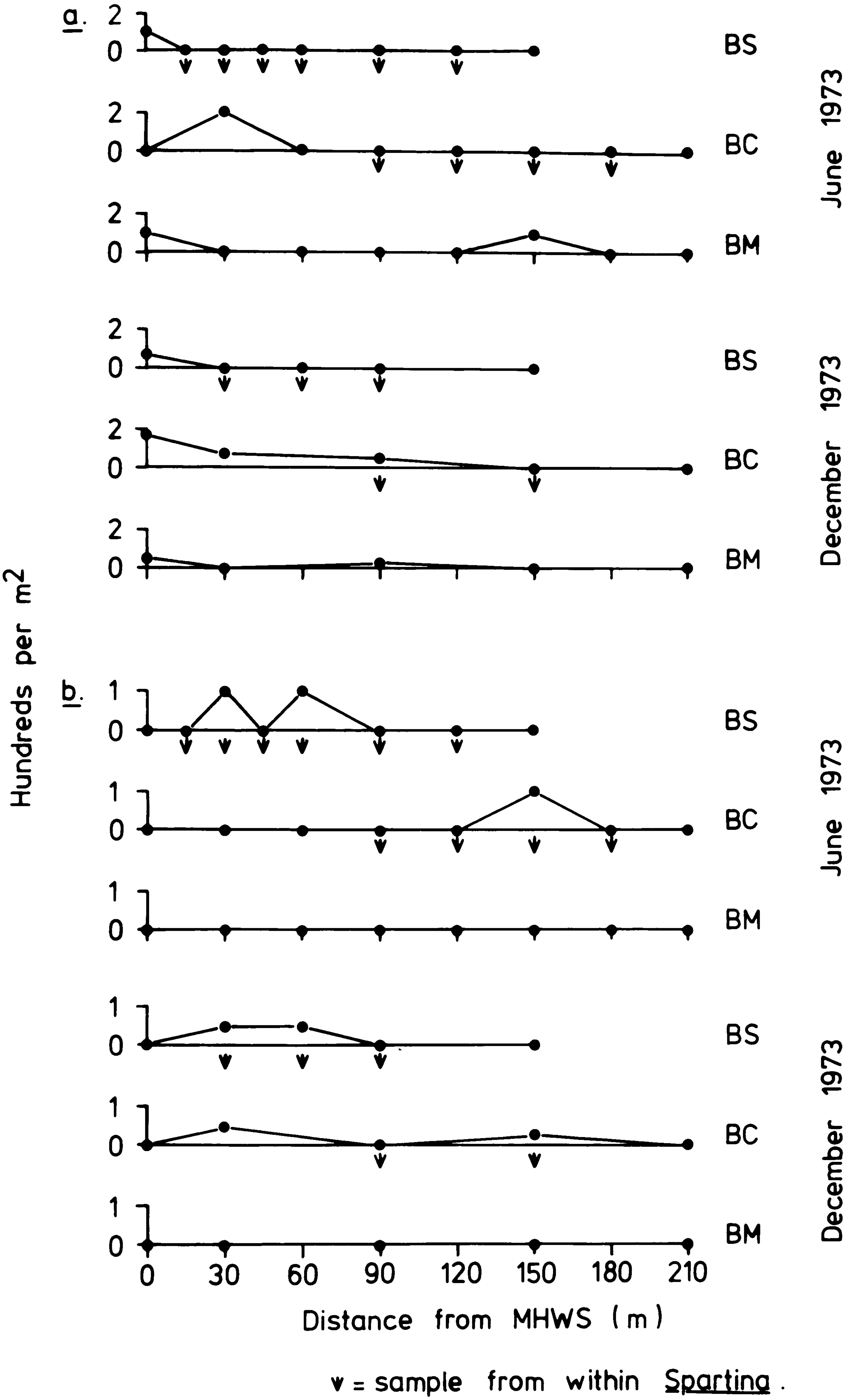


Fig. 24. Density of a. *Nereis diversicolor* and b. *Carcinus maenas* at Site B.

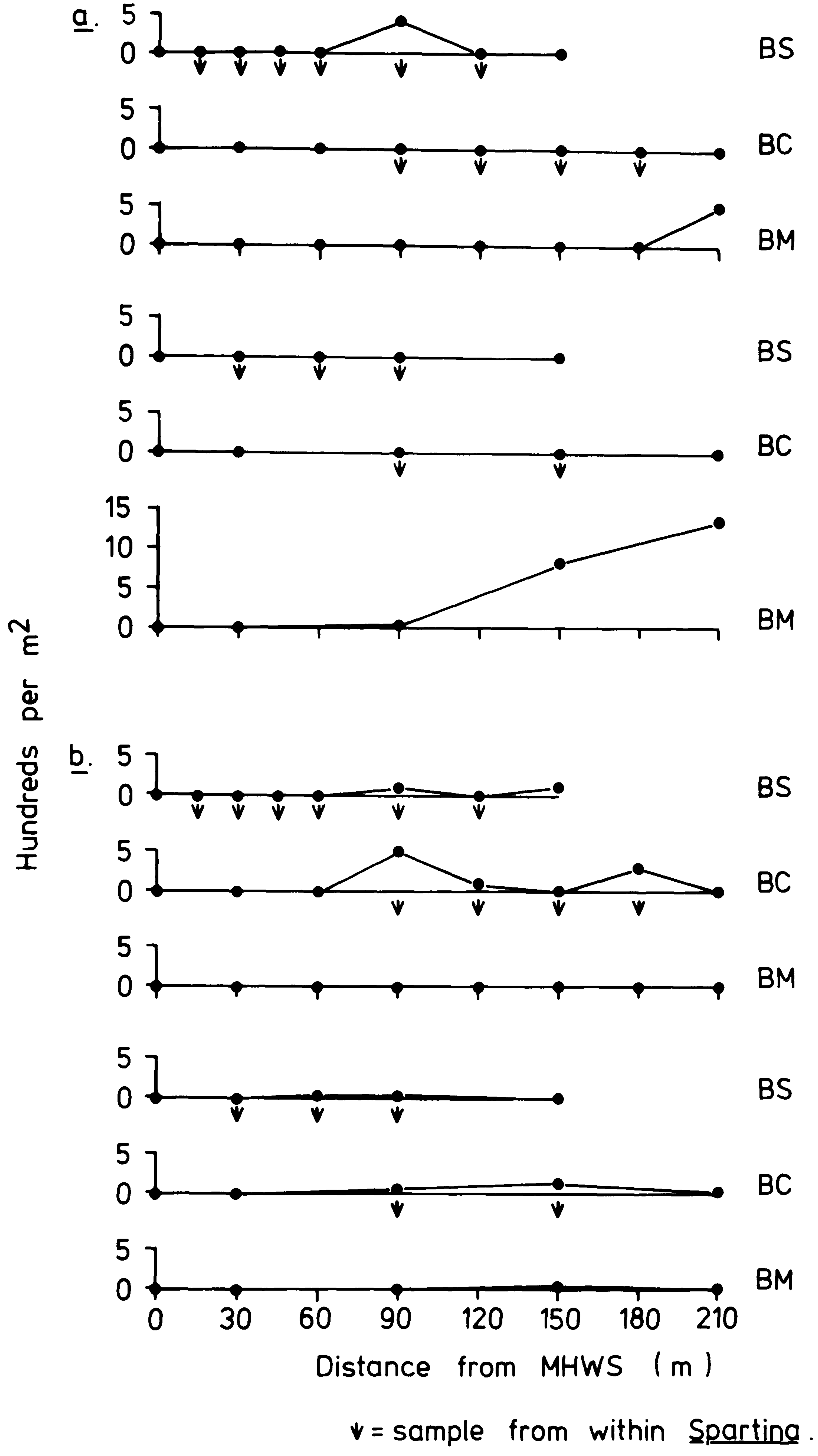


Fig. 25. Density of a. *Scoloplos armiger* and b. *Littorina saxatilis* at Site B.

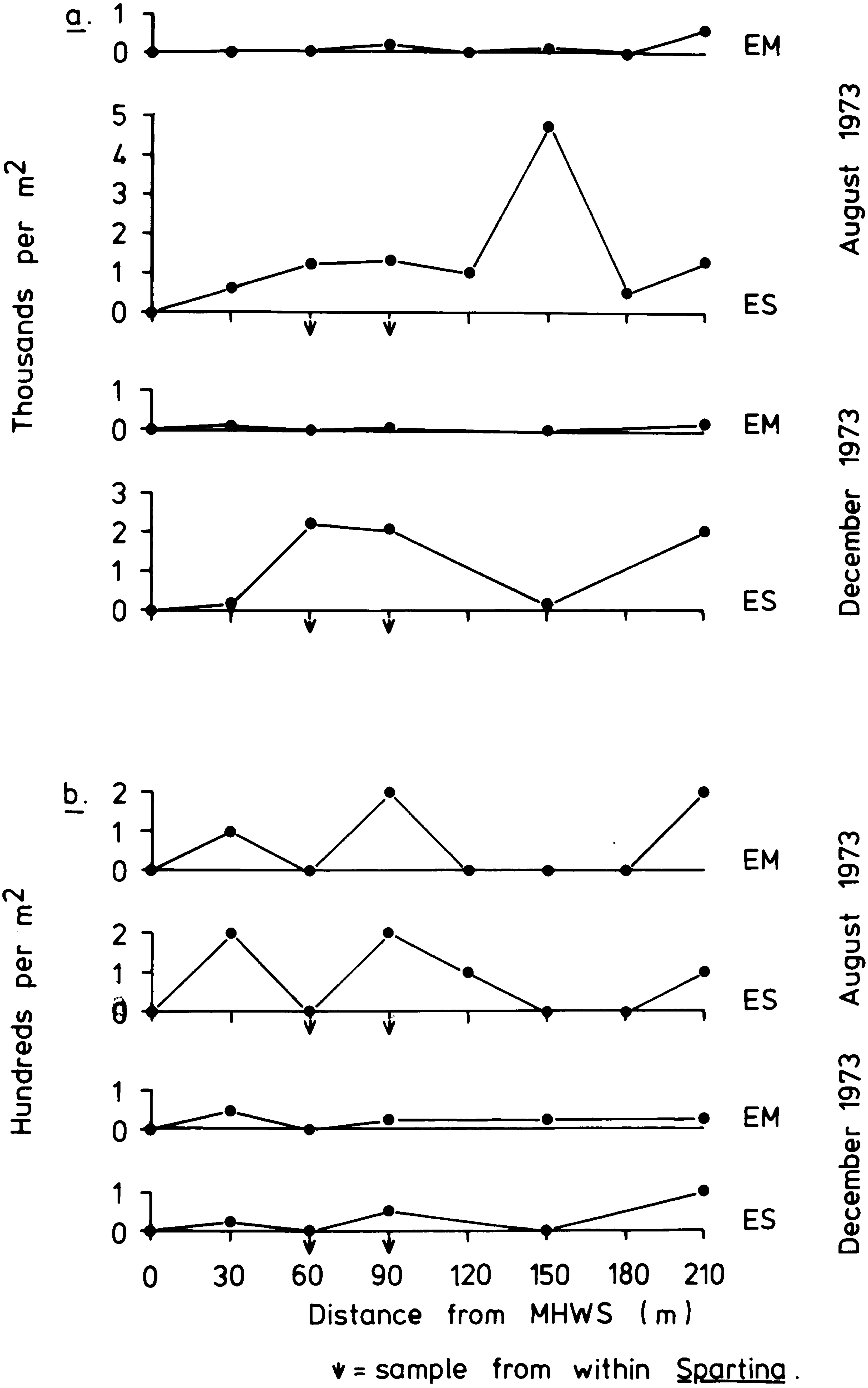


Fig. 26. Density of a. *Hydrobia ulvae* and b. *Macoma balthica* at Site E.

Macoma balthica (Fig. 26b): -

Densities and distributions of _Macoma_ in open mud were very similar to those in _Spartina_, both in August and December. In December however, there was an overall reduction in _Macoma_ density in all areas.

Littorina "saxatilis" (Fig. 27a): -

Littorina was found only on the _Spartina_ transect. Highest densities were found within _Spartina_ clumps as well as between them. Densities in December were smaller than in August.

Scoloplos armiger (Fig. 27b): -

In both August and December _Scoloplos_ densities were higher in the open mud than at the corresponding tidal levels along the _Spartina_ transect, with one exception (ES 180 in August). Within the _Spartina_ clumps _Scoloplos_ was present only in one of the two samples (ES 90) and then only at very low densities.

Arenicola marina (Fig. 28a): -

Arenicola was present in varying densities both within the _Spartina_ clumps and in the open mud. _Arenicola_ was not found beyond 90 m from MHWS in December.

Carcinus maenas (Fig. 28b): -

Carcinus was found only within _Spartina_ clumps, both in August and December.

Nereis diversicolor (Fig. 28c): -

In both August and December, _Nereis_ was found only within the first 90 m of the _Spartina_ transect.

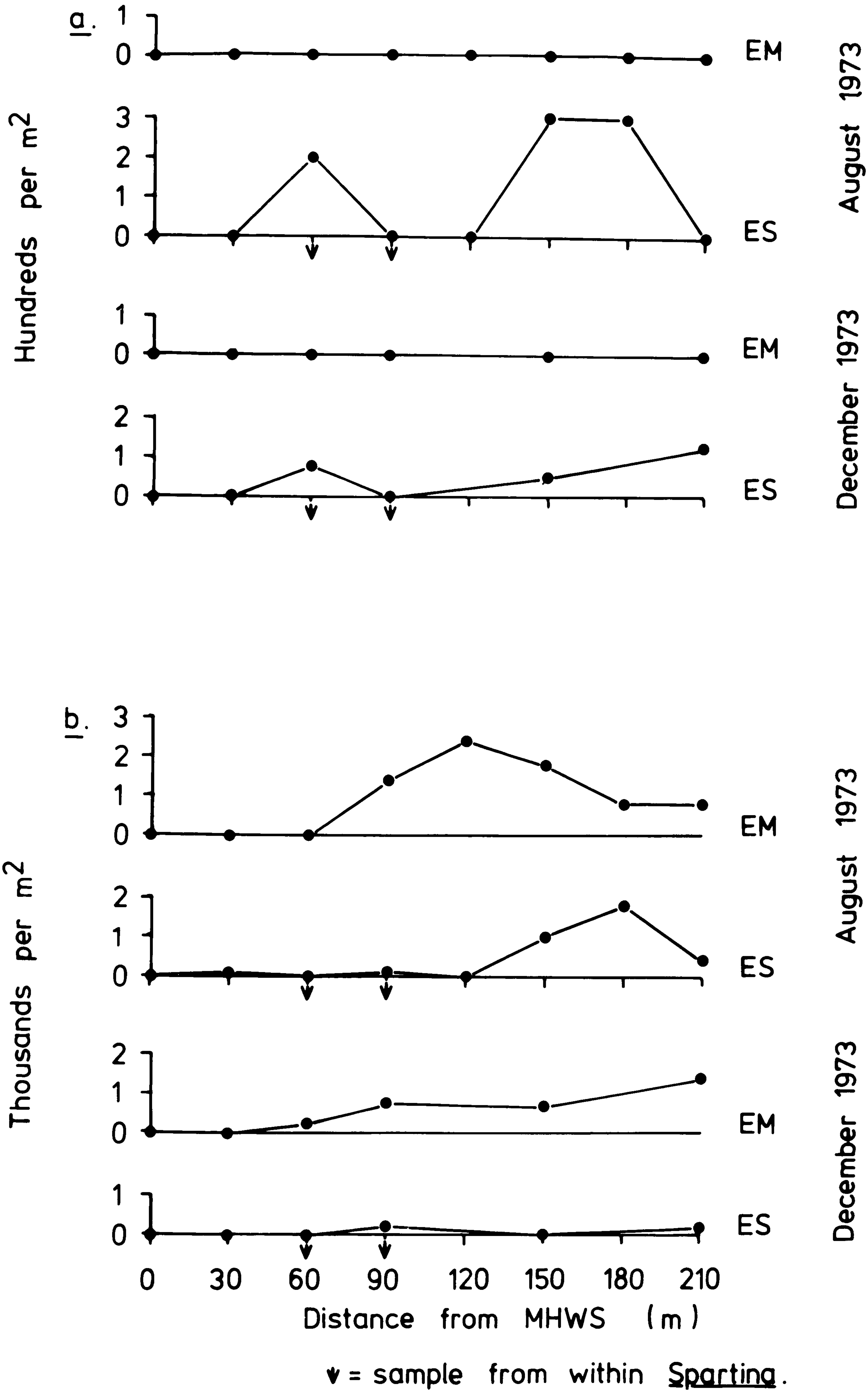


Fig. 27. Density of a. *Littorina saxatilis* and b. *Scoloplos armiger* at Site E.

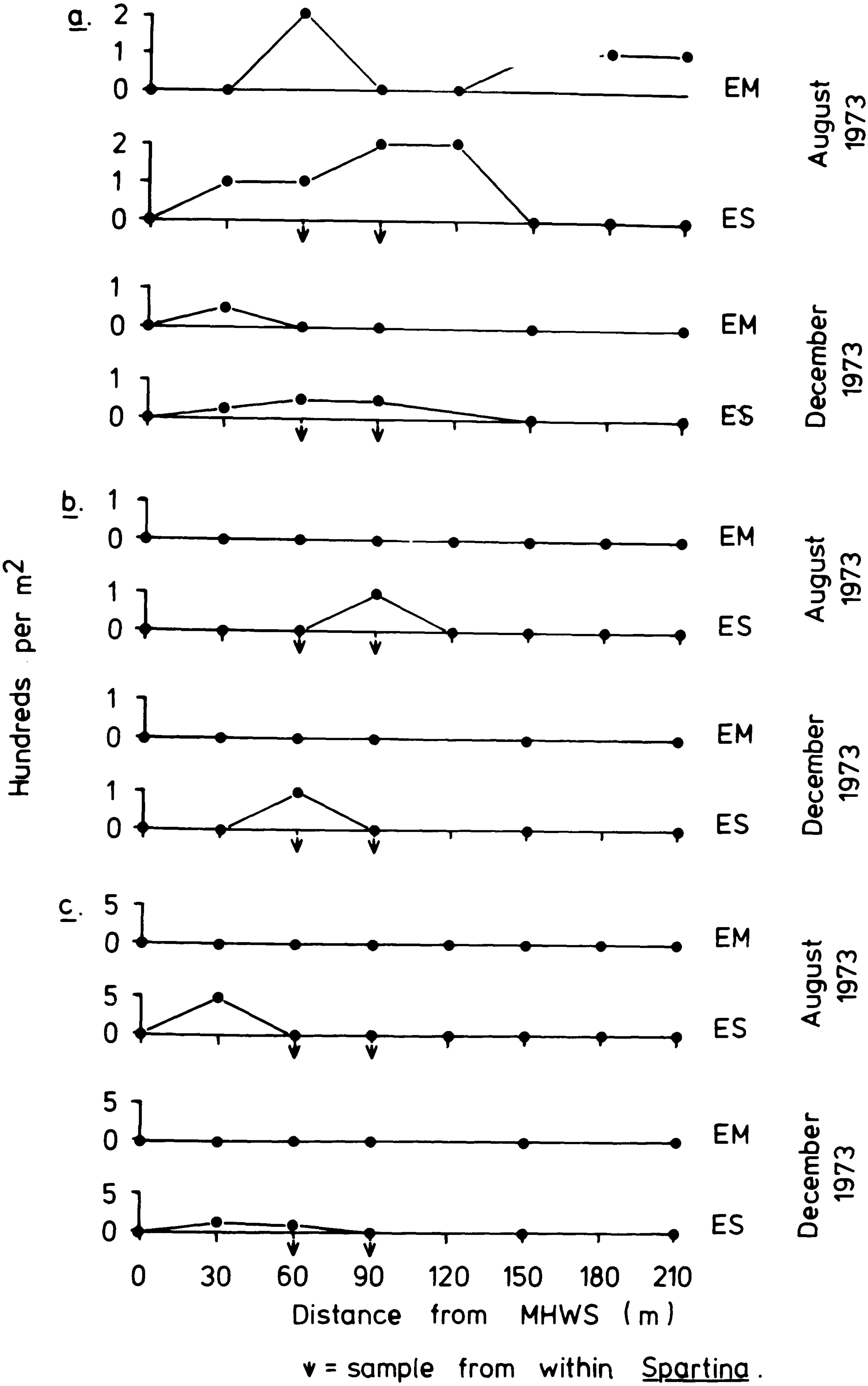


Fig. 28. Density of a. *Arenicola marina*, b. *Carcinus maenas* and c. *Nereis diversicolor* at Site E.

c. Fenham Mill and Site W.

The growth of *Spartina* at Fenham Mill formed a sward, extending approximately 60 m from MHWS, interspersed with a few small patches of open mud. Although no measurements were made of sediment characteristics, superficial examination suggested they were similar to those found along transect BS, viz., high silt, carbon, nitrogen and water contents and a shallow oxidised surface layer. Results of the invertebrate survey are given in Fig. 29. *Corophium* was restricted to between 10 and 40 m from MHWS with higher densities in an intervening patch of open mud (20 m from MHWS). *Nereis* was found between 10 and 60 m from MHWS, the highest densities occurring within areas of *Spartina*. *Scoloplos* occurred beyond 50 m from MHWS and was restricted to areas of open mud. Similarly both *Hydrobia* and *Arenicola* were restricted to the open mud beyond 60 m from MHWS. *Littorina* was found both within *Spartina* and in the open mud beyond.

At Site W, the *Spartina* extended as an uninterrupted sward from 15 to 65 m beyond MHWS. Again the sediment characteristics superficially resembled those at Site B (transect BS). Results are given in Fig. 30. *Corophium* was found only within *Spartina* and was restricted to the upshore end of the sward. While *Carcinus* was restricted also to within the *Spartina* sward, *Nereis* occurred throughout the sward and in the mud beyond.

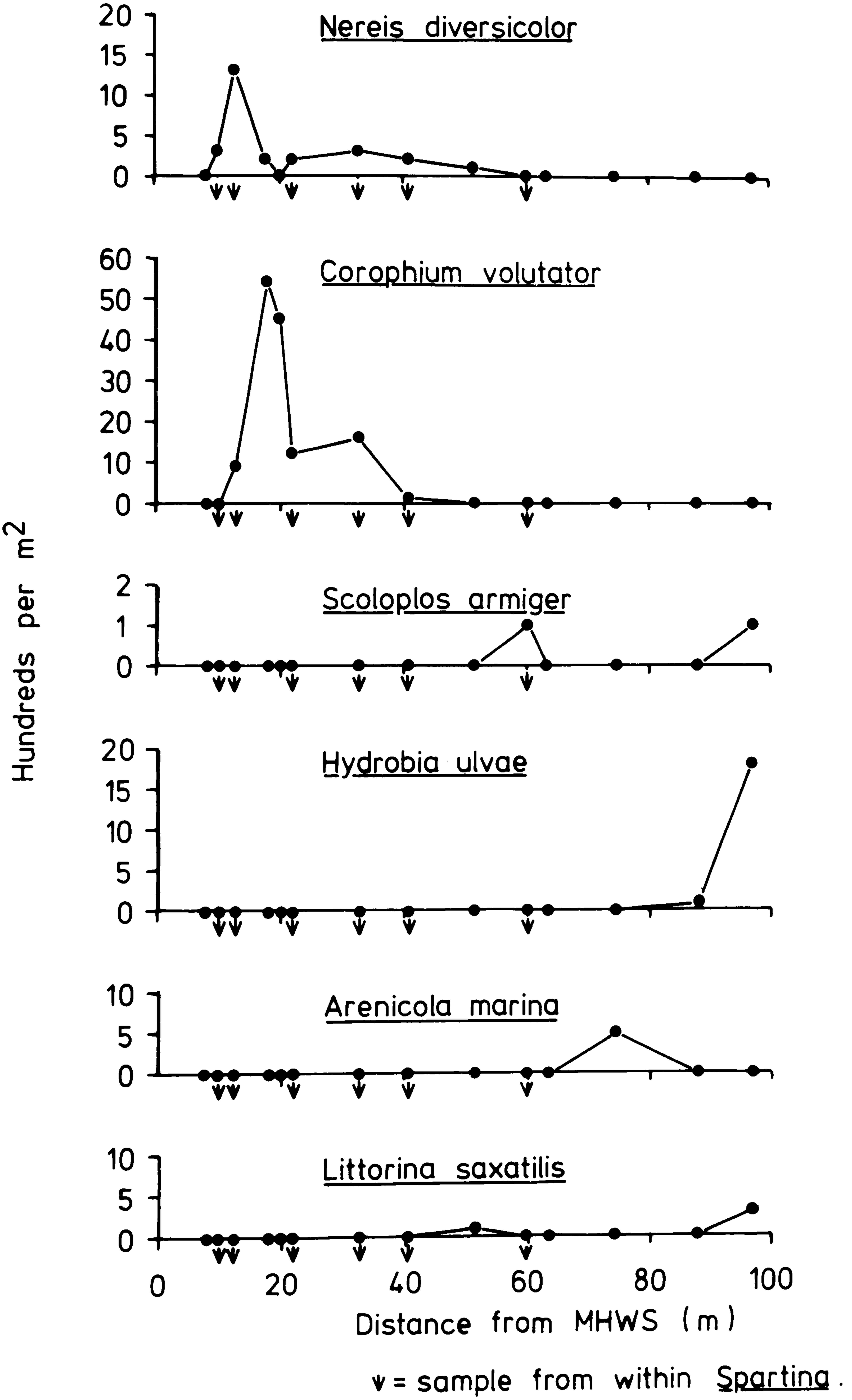


Fig. 29. Density of invertebrates at Fenham Mill.

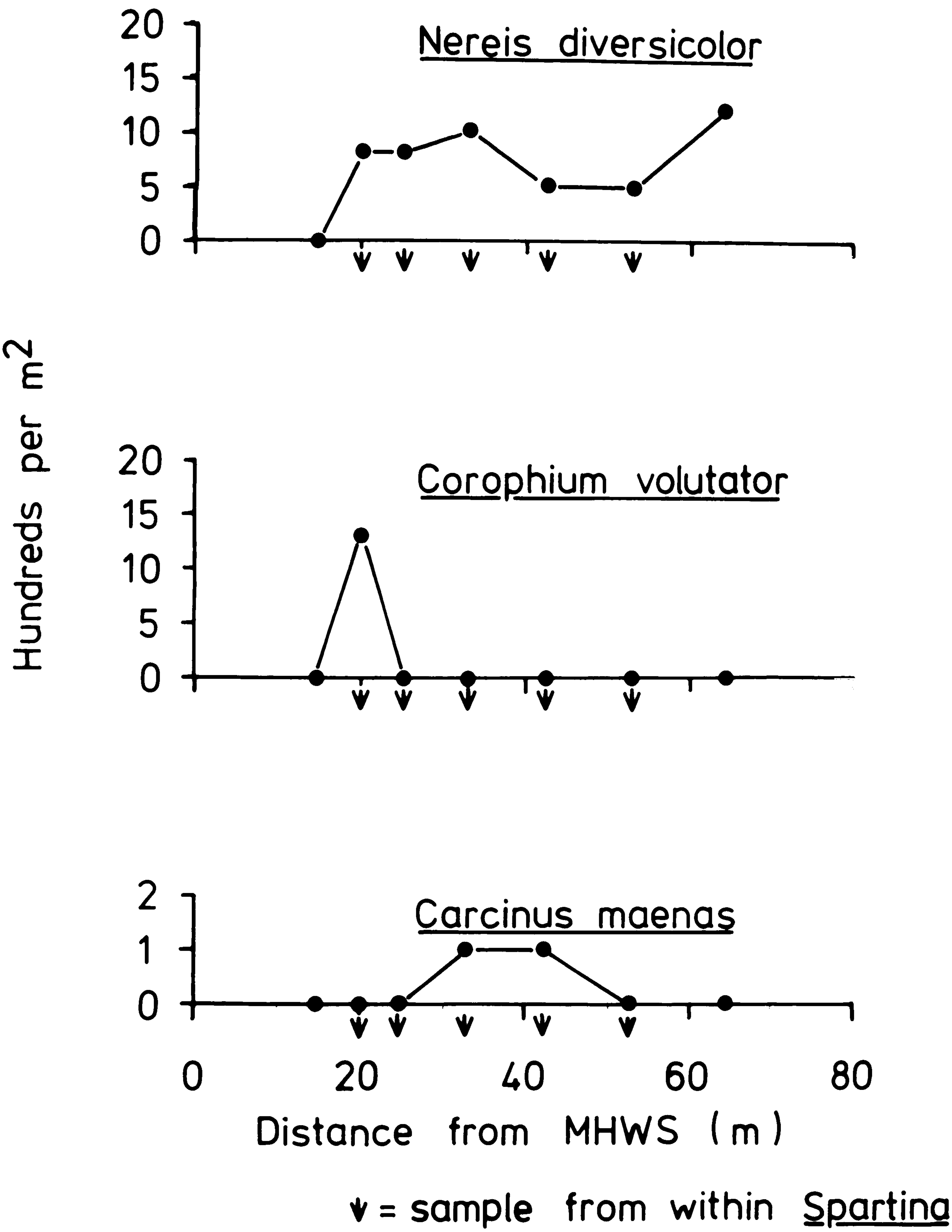


Fig. 30. Density of invertebrates at Site W.

CHAPTER 5. DETAILED STUDY OF COROPHIUM VOLUTATOR

i. Mean sizes of animals inside and outside *Spartina*.

Measurements were made of the lengths of all animals collected from the three Site B transects in December 1973 (see Chapter 4.iii., p42). In May 1974, samples were collected from those stations which had held *Corophium* in December. In those cases in which the distribution had changed between December and May so that *Corophium* were no longer present, additional May samples were collected from stations with *Corophium*, adjacent to the December stations. The mean length of each animal was measured from the tip of the rostrum to the tip of the telson.

Results: -

Histograms of size distribution were prepared for all animals taken within, and all taken outside, the *Spartina*, in both December and May (Fig. 31). As may be seen, all distributions were unimodal and not markedly skewed. Hence t-tests between means are appropriate.

Mean lengths ($\pm$ 2 S.E.s) were calculated for each sample (Table 14). Comparisons, both amongst transects, and between seasons, were frustrated in part by the temporal and spatial differences in *Corophium* distribution. However, considering all animals, there was a highly significant increase in length between December and May ($t = 48.81$, $P<0.001$). In both months the mean lengths of *Corophium* were greatest within areas of *Spartina*. In December the mean lengths of *Corophium* from *Spartina* stations were significantly greater than those from any of the four stations outside the *Spartina*. Also, in May, *Corophium* from the only *Spartina* Station (BS 30) were significantly longer than

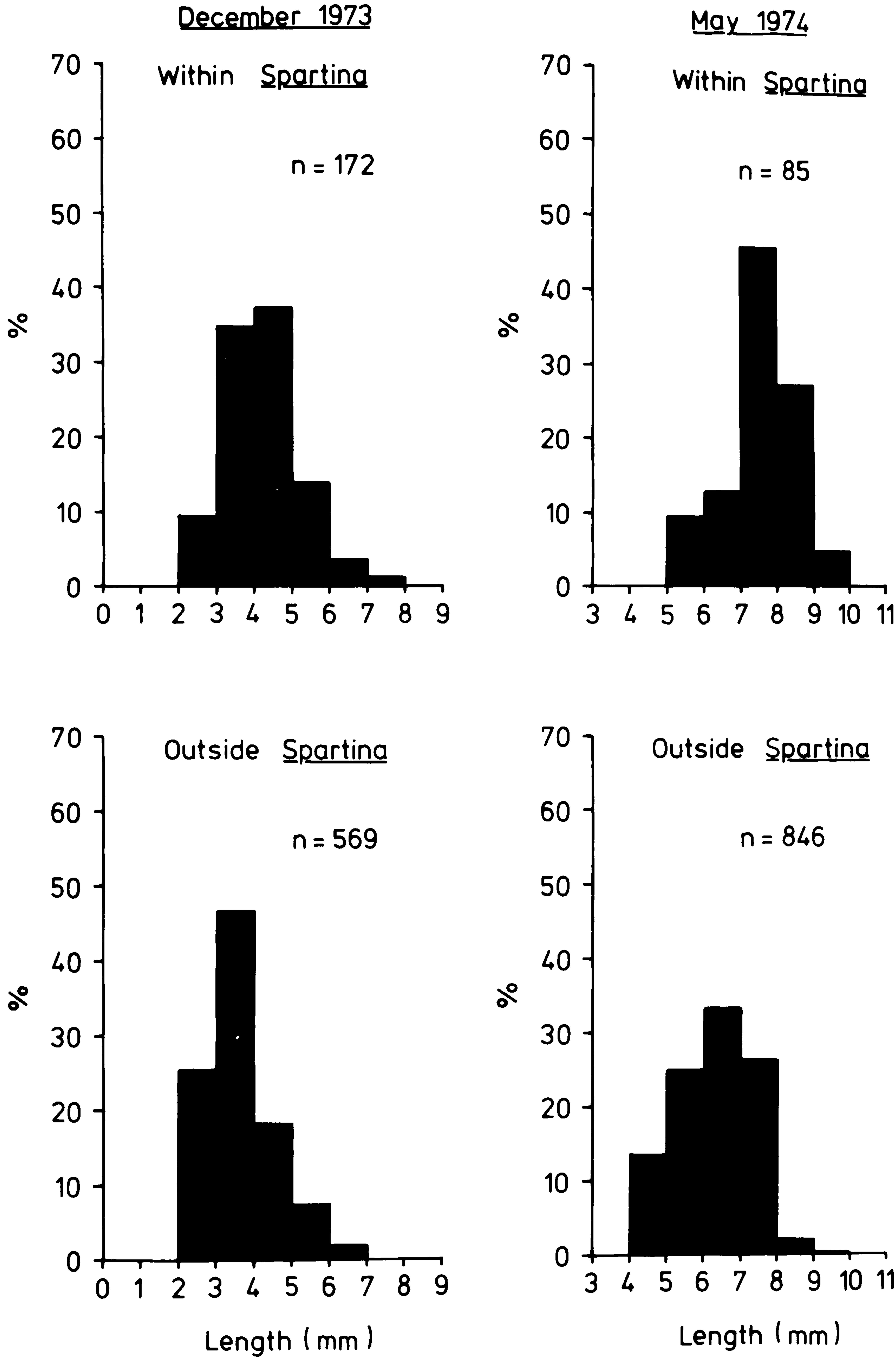


Fig. 31. Histograms of size distribution for *Corophium volutator* at Site B.

TABLE 14

Mean lengths ($\pm$ 2 S.E.s) of Corophium volutator (in mm) at Site B. Sample sizes (n) are given and those from within Spartina are indicated by *. Results of statistical comparisons between individual samples are given below.

	Transects	Distance from MHWS (m)				Overall mean
		0	30	60	90	
December 1973	BS	3.57 $\pm$ 0.40 n = 27	4.28 $\pm$ 0.27* n = 54	-*	-*	
	BC	3.65 $\pm$ 0.12 n = 281	3.68 $\pm$ 0.20 n = 113	-	4.18 $\pm$ 0.19* n = 118	3.77 $\pm$ 0.07
	BM	3.57 $\pm$ 0.12 n = 148	-	-	-	
May 1974	BS	5.79 $\pm$ 0.14 n = 230	7.35 $\pm$ 0.49* n = 85	-*	-*	
	BC	-	6.23 $\pm$ 0.13 n = 261	6.72 $\pm$ 0.23 n = 32	-*	6.38 $\pm$ 0.08
	BM	-	6.57 $\pm$ 0.14 n = 170	6.74 $\pm$ 0.12 n = 153	-	

December 1973
(BS 30* and BC 30: - $t = 3.586$, $P < 0.001$
(BC 90* and BC 30: - $t = 3.612$, $P < 0.001$

May 1974
(BS 30* and BC 60: - $t = 2.331$, $P < 0.05$
(BS 30* and BM 60: - $t = 2.423$, $P < 0.05$
(BS 0 and BC 30: - $t = 4.591$, $P < 0.001$

those from any of the five stations outside the Spartina. However, there were also variations between the lengths of Corophium from the five stations outside Spartina. In particular, those from station BS 0 were significantly shorter than those from the other four stations.

ii. Mean dry weights of animals inside and outside Spartina

Corophium collected in both December 1973 and May 1974 were sorted according to size and sampling station, and were then deep frozen until required. Animals were grouped to form a single sample of known number for each size class of a station. This was necessary to maximise weight differentials between samples. Numbers of individuals per sample varied widely, with particularly low numbers in the larger size classes. However, no minimum limit was set as it was considered necessary to maximise the information obtained from the specimens. Samples were dried in a vacuum oven at 60°C for 72 hours and then weighed on an electric microbalance.

Results: -

Untransformed weights are given in Appendix 3, p139. A single mean weight was calculated for each size class in each of the two habitats (Spartina sward and open mud) as shown below: -

e.g. Size class:- 3 mm - 4 mm, Habitat:- open mud.

Samples involved	Mean weight		No. of individuals	
BS 0	0.0981	x	8	= 0.7848 mgm
BC 0	0.0821	x	136	= 11.1610 mgm
BC 30	0.1314	x	42	= 5.5180 mgm
BM 0	0.1362	x	80	= 10.8900 mgm
	Totals		266	28.3538 mgm

$$\text{Overall Mean} = \frac{28.3538}{266} = 0.1066 \text{ mgm}$$

This method of calculating overall means was adopted to take account of the widely varying sample sizes used. The resulting mean weights were plotted against lengths on a double logarithmic scale (Fig. 32).

In December 1973 the mean weight inside Spartina was greater than outside for the five size classes with comparable data. The probability of this occurring by chance is 1 in 2^5 (P = 0.03) and hence the difference is statistically significant. In May 1974 the mean weight inside Spartina was greater than outside for three size classes and less than outside for one. The probability of this occurring by chance is 4 in 2^4 (P = 0.25) and hence the difference is not significant.

Since Corophium are scarce within Spartina the overall means for this habitat are based on fewer animals than those for outside Spartina. This has been noted when considering the validity of the results in the discussion.

iii. Habitat selection by Corophium.

Corophium density in relation to silt/clay content of the sediment, was investigated in summer 1973 at Site B (Fig. 33). Above a silt content of 50% Corophium was either absent or present at very low densities. Below this level, Corophium density appeared to increase with decreasing silt/clay content, though variation in density for a given silt/clay content was very wide.

Five of the six stations with silt/clay contents higher than 50% occurred within Spartina. This was noted when considering the results in the discussion.

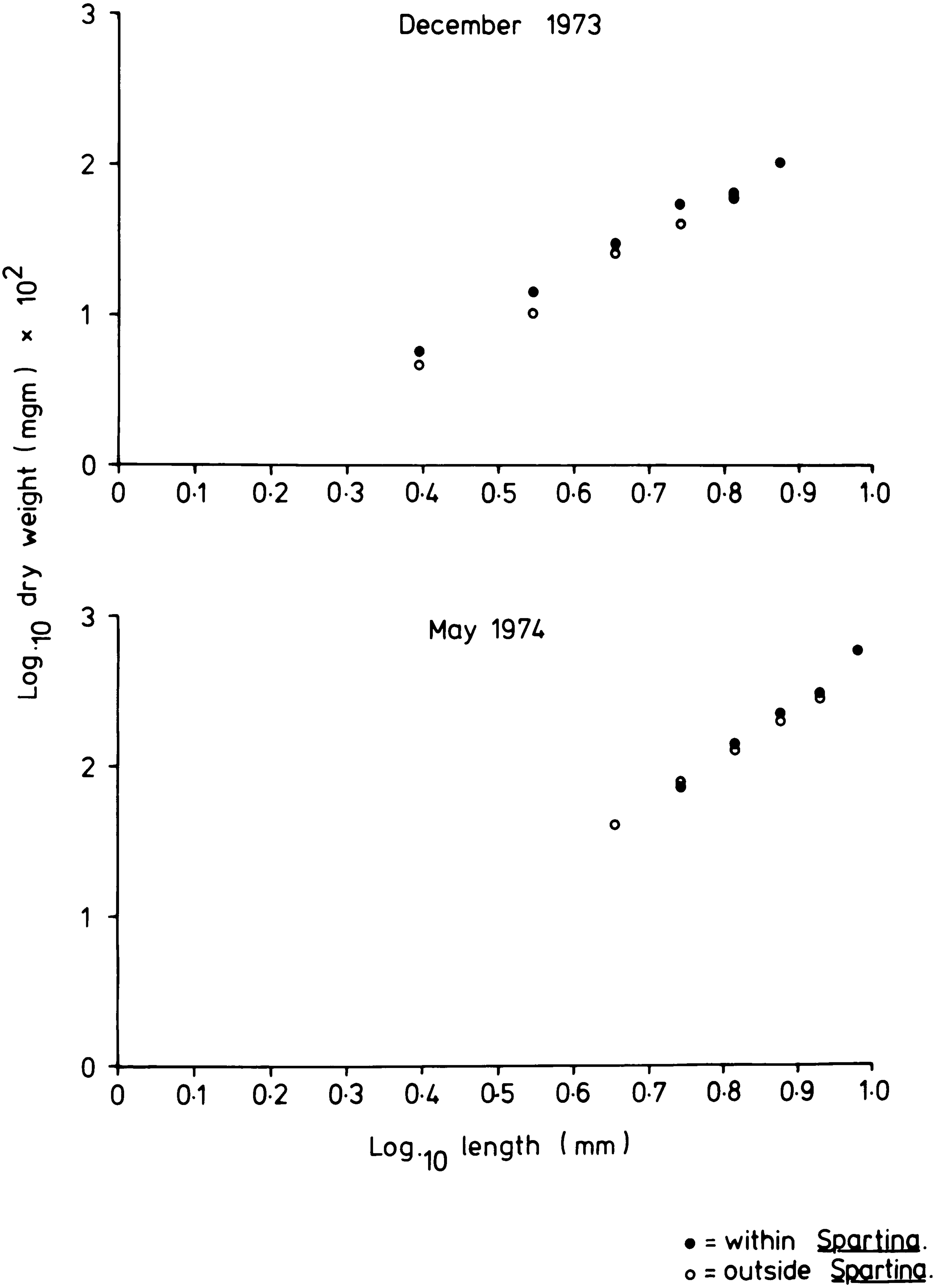


Fig. 32. Log. weights of *Corophium volutator* plotted against log. lengths at Site B.

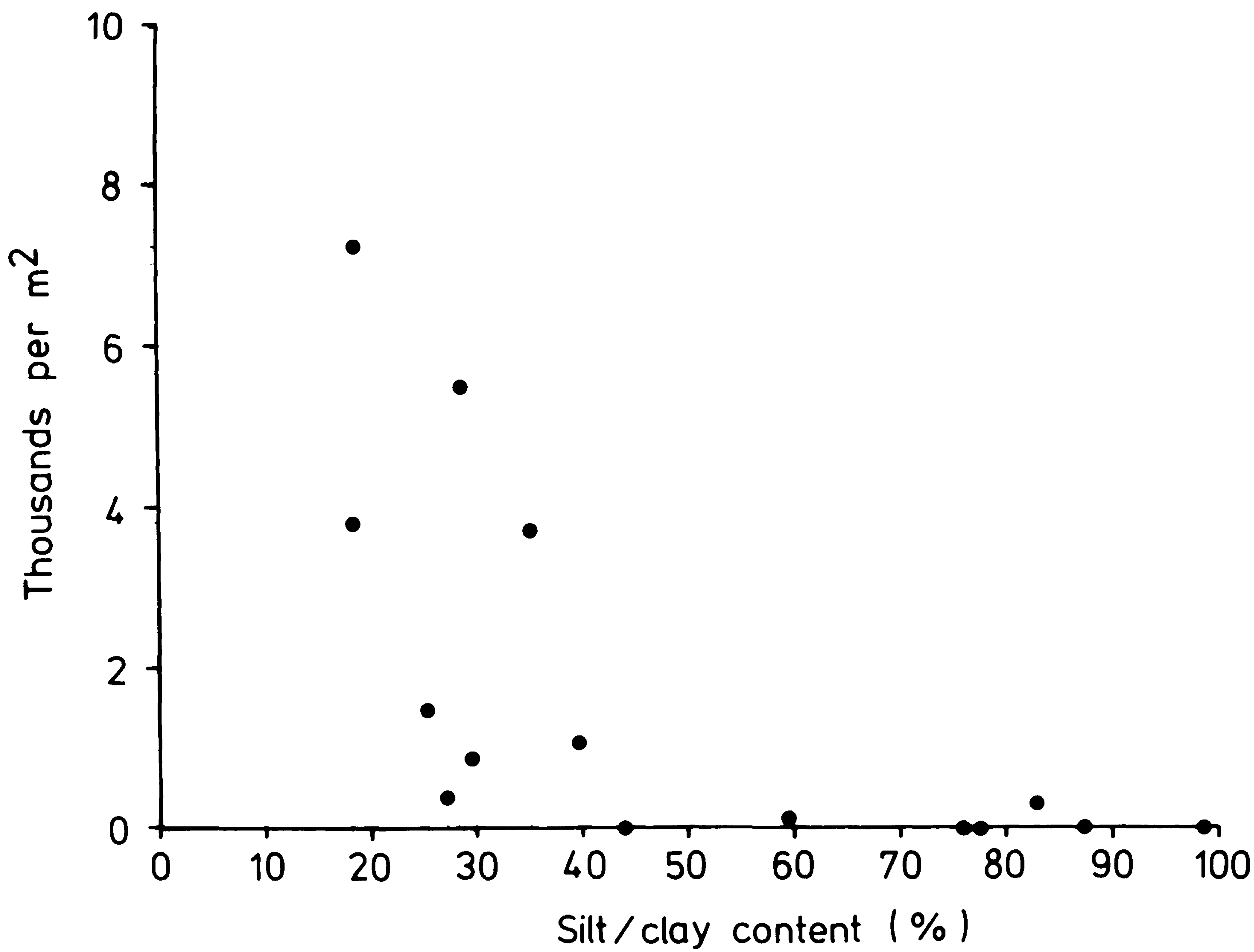


Fig. 33. Density of <u>Corophium volutator</u> plotted against silt / clay content at Site B.

iv. Behavioural response of *Corophium* to different sediment types.

Meadows (1964a) demonstrated in the laboratory that *Corophium* preferred to burrow in fine sediments rather than coarse ones. In view of the high silt/clay content within *Spartina* swards (see Chapter 3. viii. p 29) it is perhaps surprising that *Corophium* was so scarce in these areas at Lindisfarne. Therefore laboratory studies were made of the behavioural response of *Corophium* to sediments taken from within *Spartina* and from areas outside the *Spartina* where *Corophium* was already established. Experiments were conducted also in the field.

a. Two-choice preference experiment in the laboratory:-

The procedure was similar to that used by Meadows (1964a). Two crystallising dishes, 12 cm in diameter and 6.5 cm high, were each divided into two compartments using a perspex partition, 12 cm long by 4 cm high (Fig.34a). The partition was maintained in position using plasticine. The left-hand compartment of each dish was filled with sediment from transect BS, within the *Spartina* sward, and the right-hand compartment with sediment from transect BM, on the open mud. Sediment was collected on the day prior to the tests and stored at 10°C. Fresh seawater was siphoned slowly into each of the dishes until the level was 2 cm above the partition. The dishes were surrounded with black paper, placed in the 10°C (constant temperature) room and each illuminated by an angle-poise lamp, situated 40 cm directly above the dish. This was far enough above the dishes to cause negligible heating. Twenty live *Corophium* were then introduced into each dish at a constant position and direction (Fig. 34b) to avoid biassing their choice of sediments. Their behaviour (swimming, burrowing, or

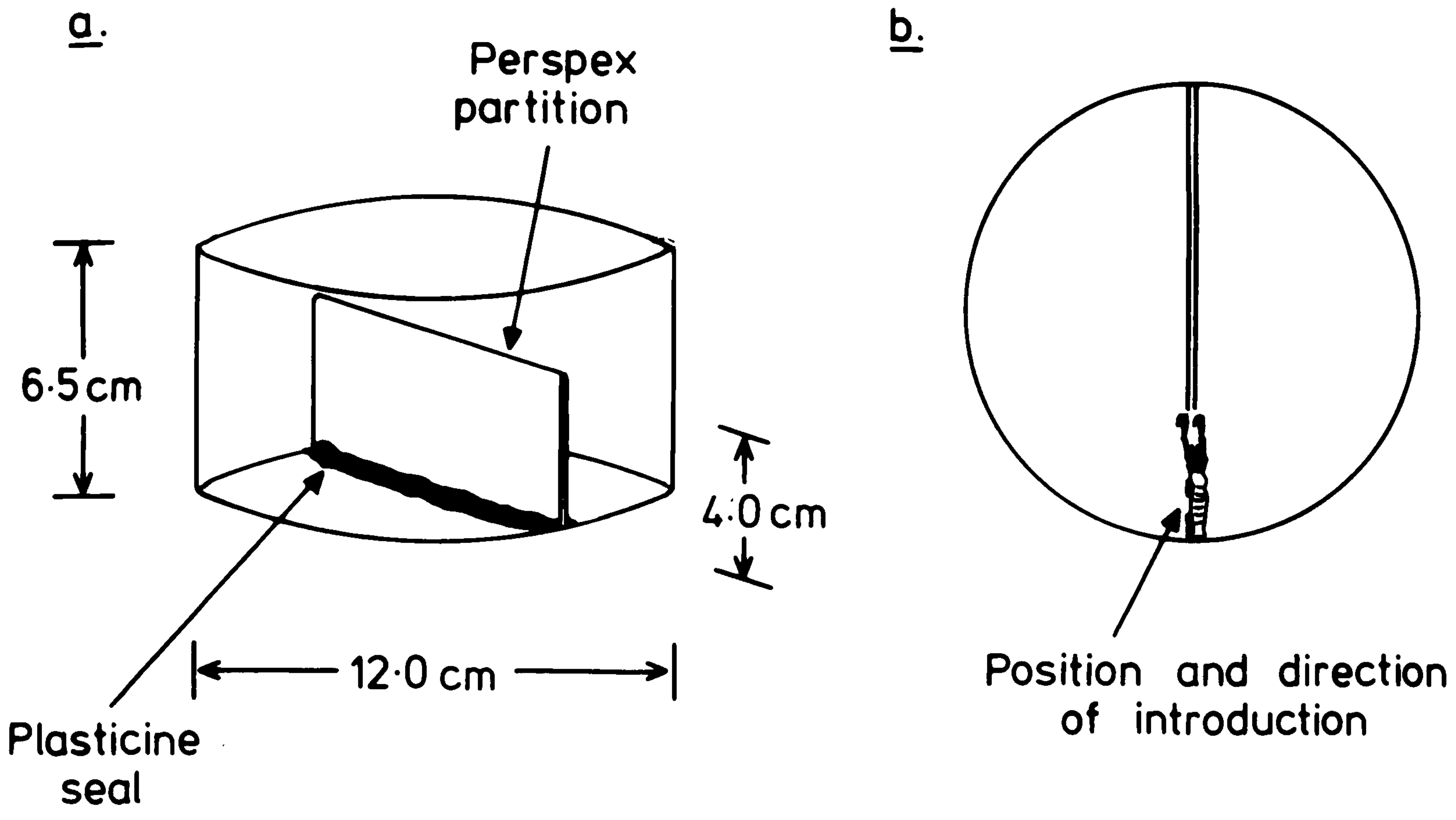


Fig. 34. Crystallizing dish for two-choice preference experiment with Corophium volutator.

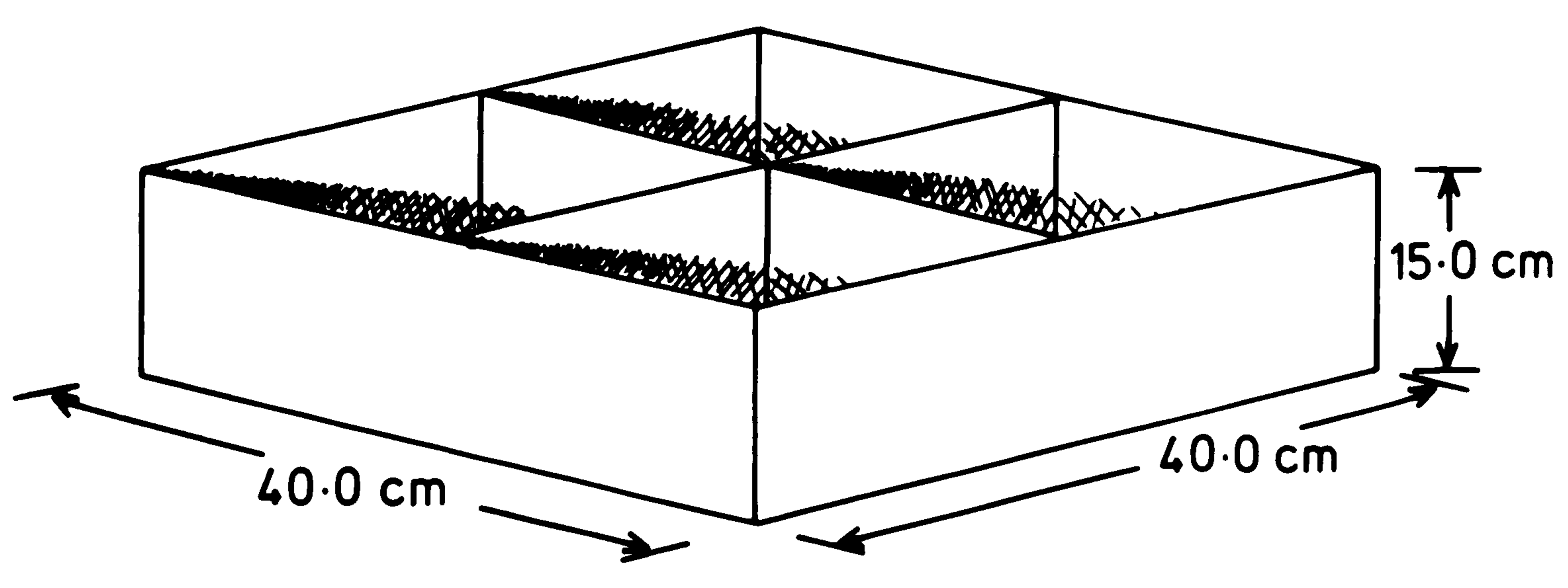


Fig. 35. Plywood enclosure for estimation of Corophium volutator settling rates in the field.

crawling on the mud surface) was noted at five minute intervals for the first fifteen minutes. Animals not observed were recorded as having burrowed into either of the sediments. The dishes were then left for a further $2\frac{3}{4}$ hours, after which the numbers of Corophium in each compartment were determined by washing through a 20 mesh per inch sieve.

Results (Table 15): -

No significant difference was found between the numbers of Corophium burrowing into the two types of sediment, although in both dishes more Corophium burrowed into the Spartina sediment than into the open mud sediment. Some movement of Corophium was observed across the partition, indicating that individuals investigated both sediments before selecting one to burrow in. It is possible that chemical changes (e.g. reduction of hydrogen sulphide content of Spartina mud) occurred between collection of the mud in the field and its use in the laboratory. Field experiments were therefore performed to avoid this possible artefact.

b. Settling rates in the field: -

A plywood enclosure, partitioned into four equal sized sections, was used (Fig. 35). The enclosure was placed on the sediment when the falling tide was at a depth of between 5 cm and 10 cm. (When the depth was greater than this it was difficult to see clearly the behaviour of Corophium on or near the sediment surface). Small cracks in the joints enabled the water level in the enclosure to fall with the tide as it ebbed. Corophium were collected immediately prior to high water by washing mud samples from transect BM through a 20 mesh per inch sieve. The animals used were all between 5 mm and 8 mm long.

TABLE 15

Results of *Corophium volutator* two-choice preference experiment carried out in the laboratory. At the end of the experiment the total number of *Corophium* within the *Spartina* sediment from both dishes was compared with that in the open mud sediment and the Chi^2 value was found to be 2.5 ($P > 0.05$, with 1 degree of freedom).

Sw = swimming; Bu = burrowing; Cr = crawling on surface of mud

Minutes after introduction of *Corophium*	DISH 1							DISH 2						
	Sediment from *Spartina*			Sediment from open mud			Number already burrowed	Sediment from *Spartina*			Sediment from open mud			Number already burrowed
	Sw.	Bu.	Cr.	Sw.	Bu.	Cr.		Sw.	Bu.	Cr.	Sw.	Bu.	Cr.	
5	3	-	-	2	-	2	13	3	1	1	2	-	2	11
10	1	-	2	-	1	1	15	4	1	2	3	1	-	9
15	1	-	6	-	-	1	12	4	-	2	-	1	-	13
180	Total number present = 14			Total number present = 6				Total number present = 11			Total number present = 9			

Corophium behaviour was observed among *Spartina* (transect BS) in areas uncolonised by *Corophium* and on the open mud on transect BM. Ten *Corophium* were introduced into each compartment and the number observed swimming was noted at regular intervals until all had settled on the sediment surface or the tide had ebbed beyond the enclosure. This was repeated on several days in each of the areas.

Results: -

Individual observations are given in Appendix 3, p 140. For each observation the total numbers of *Corophium* swimming in the four compartments of the enclosure were summed and calculated as a percentage of the number originally introduced. A mean was calculated for all observations made in each successive time interval after intoduction (Table 16). As a result of the tide ebbing beyond the enclosure and in some cases all the *Corophium* burrowing, only a small number of observations were made in the later time intervals.

In transect BM *Corophium*, already present in the sediment, often emerged from their burrows and joined the animals being observed. Despite the presence of these additional animals, there was a tendency, albeit non-significant, for a greater percentage of *Corophium* introduced to remain swimming above the *Spartina* sediment than the open mud sediment.

v. Winter predation of *Corophium*: An exclosure experiment

A wire-netting exclosure (Fig. 36) was used to prevent birds and flat-fish from feeding on a 5 m^2 area of mud at Site B, approximately 25 m downshore from MHWS along transect BM (Fig. 2). It was placed in position on 29/10/73. Eight 10 cm x 10 cm x 10 cm

TABLE 16

Mean percentage ($\pm$ 2 S.E.s) of *Corophium* swimming above *Spartina* and open mud sediments in the field experiment at Site B. Mean percentages from equivalent time intervals were compared and values of t are given.

n = total number of observations made during a particular time interval.

Minutes after introduction of *Corophium*	*Spartina* (transect BS) Mean percentage of *Corophium* swimming	n	Open mud (transect BM) Mean percentage of *Corophium* swimming	n	t	P
1 - 4	30.50 $\pm$ 9.76	15	16.25 $\pm$ 11.10	4	1.93	>0.05
5 - 8	17.83 $\pm$ 15.20	8	14.18 $\pm$ 14.20	3	0.351	>0.05
9 - 12	18.23 $\pm$ 24.76	3	12.50	2	0.463	>0.05
13 - 16	15.63 $\pm$ 27.36	4				
17 - 20	0.83 $\pm$ 1.68	3	-	1		

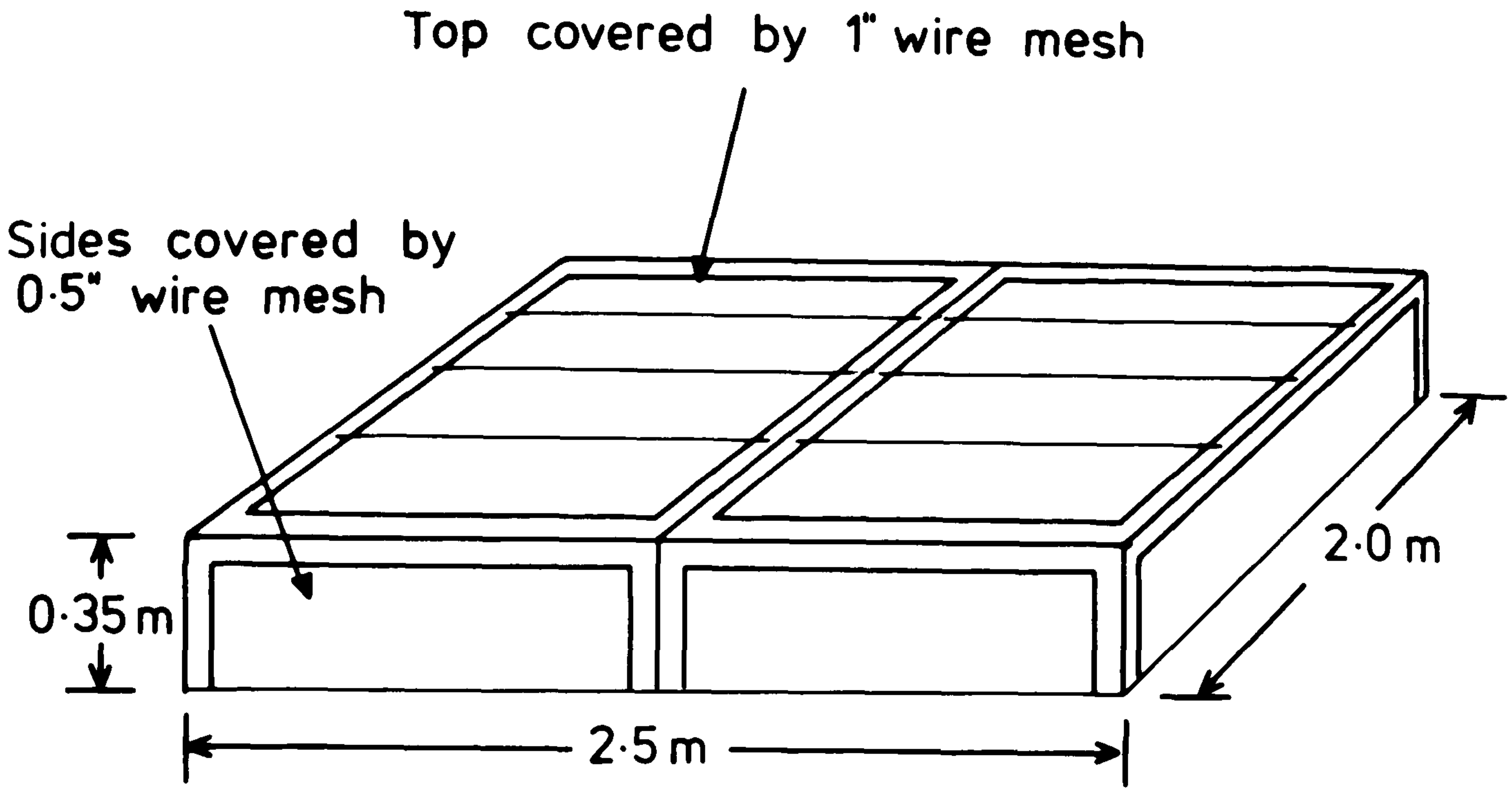
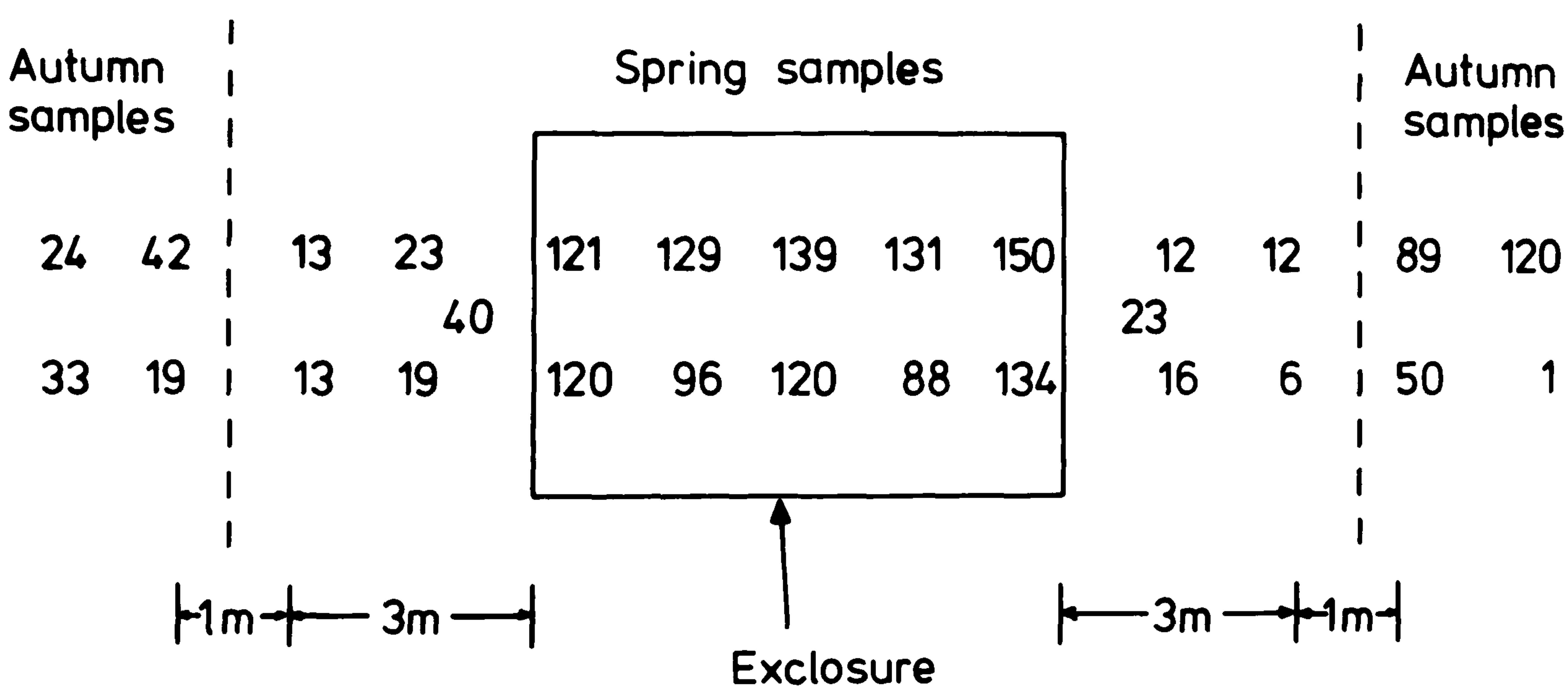


Fig. 36. Exclosure.



Autumn mean density = 4725 ± 2772 per m^2
Spring mean density inside exclosure = 12280 ± 1188 per m^2
Spring mean density outside exclosure = 1770 ± 598 per m^2

Fig. 37. Results of Corophium volutator exclosure experiment at Site B.

mud samples were collected to determine *Corophium* density in the area at that time. The exclosure was removed on 29/3/74 when ten samples were collected from within its boundary and ten from outside. All samples, both in autumn and spring, were collected: - a) from the same tidal level to avoid any downshore variation in *Corophium* density; b) at a minimum distance of 2 m from the exclosure since birds were not observed feeding immediately adjacent to it. Autumn samples were collected 1 m out from the spring sites to avoid disturbing them. Additionally, in March, three samples of the surface layer of sediment, 1 cm deep, were collected from within the exclosure and mixed thoroughly. Another three were collected approximately 2 m from the exclosure. Carbon content and particle size of these samples were determined as described in Chapter 3, vi. (p 25) and viii. (p 29).

All *Corophium* extracted from the samples by sieving were measured and assigned to size classes. Any filamentous alga present in the spring mud samples was removed during the sieving, dried in a vacuum oven at 60°C for 72 hours and weighed.

Results: -

The numbers of *Corophium* in each sample associated with the exclosure are given in Fig. 37, together with mean densities. No significant differences were found between the autumn mean density and the spring mean density outside the exclosure ($t = 2.085$, $P > 0.05$). The spring mean density inside the exclosure was significantly greater than the spring mean density outside ($t = 7.902$, $P < 0.001$), and the autumn mean density ($t = 2.504$, $P < 0.05$).

Since the change in *Corophium* density outside the exclosure during the winter season was not significant, either mortality was small or it was balanced by recruitment or immigration. By the spring, the *Corophium* density within the exclosure was approximately seven times that found outside. If predation outside the exclosure had been responsible for this difference, then between approximately 7.5 and 10.5 thousand *Corophium* per m^2 (75 to 105 million per ha) must have been taken during the time the exclosure was in position. But observations of Redshank (Chapter 7. iv. p 97), the chief bird predator, showed that less than 3 million items of *Corophium* size were taken per ha during the same time period.

Breeding of *Corophium* at Whitby was found to cease in September and recommence the following April (Hart 1930). At the more northerly Lindisfarne, it is likely that at least one month elapsed between hatching of the final autumn brood and the October sampling. Hence the majority of the final brood would have grown large enough to be retained by the 30 mesh per inch sieve used. It seems probable therefore, that the increased density within the exclosure must have resulted from an immigration of *Corophium* into the exclosure, rather than growth of animals which were too small to be retained by the sieves in the autumn.

Mean lengths of *Corophium*, both inside and outside the exclosure, were significantly greater in spring than in autumn. In addition, *Corophium* within the exclosure in spring had a significantly greater mean length than those outside (Fig. 38). Comparison of histograms *b* and *c* indicates that this was due to a much larger proportion of animals over 6 mm in length within the exclosure.

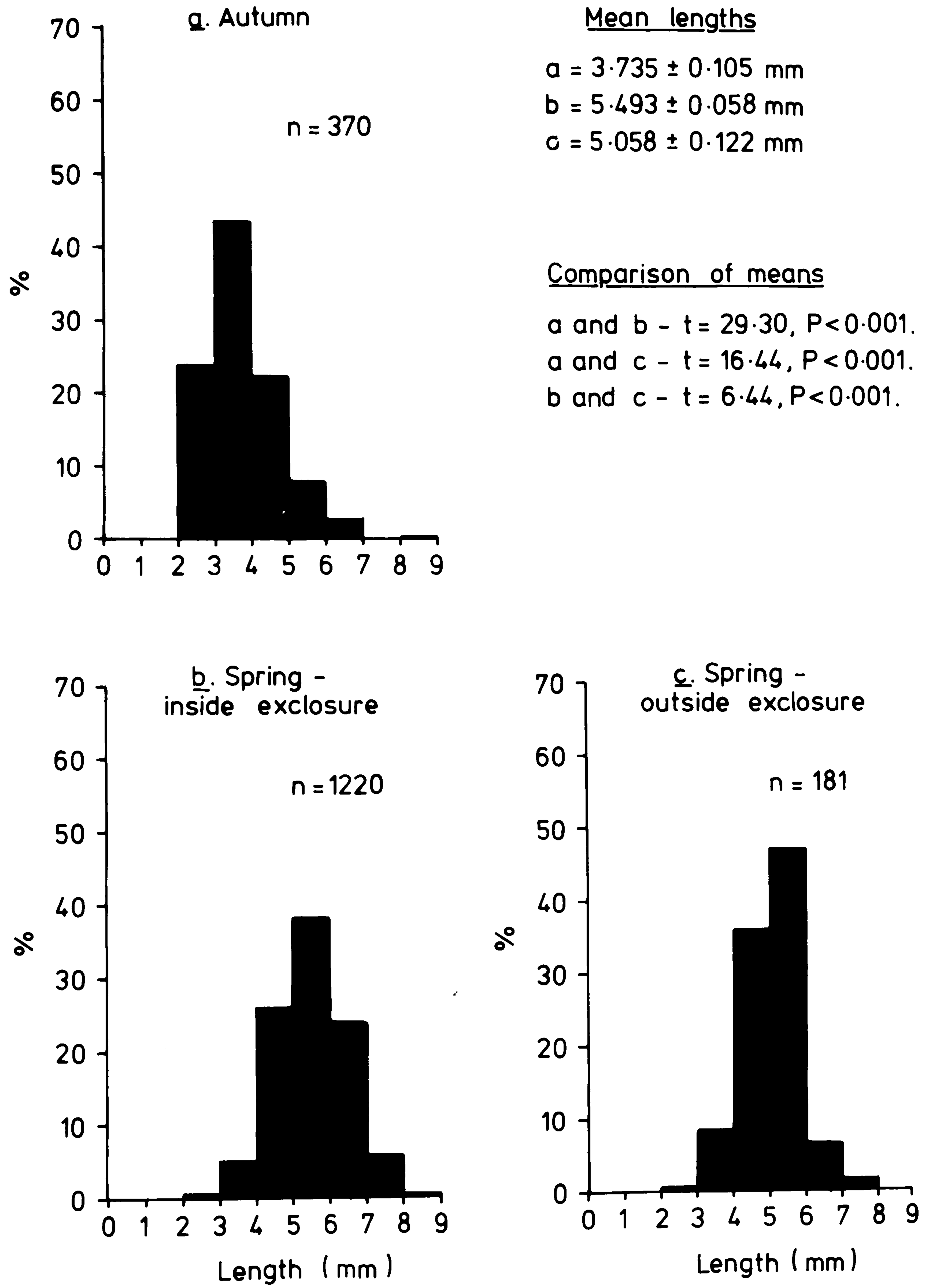


Fig. 38. Histograms of size distribution for Corophium volutator from the exclosure experiment at Site B.

There were noticeable differences between sediment inside and outside the exclosure in spring (Table 17). Inside the exclosure carbon and silt contents were higher and median particle diameter smaller than outside. These results suggest that the presence of the exclosure changed the nature of the sediment by causing accretion of fine particled silt and organic detritus.

No significant difference was found between the mean dry weights of algae from samples inside and outside the exclosure.

vi. Movement of *Corophium*

There is no reference in the literature to studies of *Corophium* movement in the field. In view of its possible influence on the exclosure results, an investigation of movement was made by marking animals within a small area and then searching for them at varying distances from the marked area.

The use of dye was considered as a means of marking *Corophium*. Previous workers have used dyes to study the movement and distribution of oyster larvae (Loosanoff and Davis 1947) and small mammals (New 1958). Peters and Chevone (1968) used neutral red in an ecological investigation of mosquito larvae. This dye was used in the present study. Barbosa and Peters (1970) showed that exposure to neutral red affected the length of development and rate of pupation in populations of *Aedes aegypti* (L.). Although no information is available on the effect of neutral red on *Corophium*, it was considered unlikely to have any serious effect in this relatively short term study.

TABLE 17

Sediment characteristics of *Corophium* exclosure on transect BM in 1973/74. Mean dry weights of alga inside and outside the exclosure were compared when t was found to be 1.269 ($P > 0.1$).

Sediment characteristic	Inside	Outside
Carbon content	3.27%	1.43%
Silt content	43.60%	28.38%
Median particle diameter	220 μ	300 μ
Mean dry weights of alga	0.116 ± 0.129 g	0.030 ± 0.038 g

a. Determination of optimum dye concentration: -

A preliminary experiment was performed to determine the optimum concentration of neutral red necessary to stain Corophium without any obvious adverse effects. Three crystallising dishes were each half-filled with fresh sediment from an area at Lindisfarne known to contain Corophium. The sediment was previously washed through a 30 mesh per inch sieve to remove all animals. After the sediment had settled for two hours, any surface water was carefully siphoned from it with a 3 mm diameter rubber tube. Neutral red dye was dissolved in fresh seawater in concentrations of 10, 50, and 100 p.p.m. Each of the three dye solutions was then siphoned into separate dishes, avoiding disturbance of the sediment as much as possible. Fifteen live Corophium were introduced into each of the three dishes and left for 5 hours. The dyed seawater was then siphoned off and replaced by fresh, uncontaminated seawater. For each of four days following the treatment, the condition of any visible Corophium was noted and the seawater was changed. During the course of the experiment dishes were aerated and kept at a temperature of 10°C. At the end of four days all animals were removed from the mud by sieving and their condition noted.

Results (Table 18): -

10 p.p.m. was clearly too dilute to stain the animals effectively. No difference was observed between animals stained by the 50 and 100 p.p.m. solutions. It was therefore decided to use neutral red at a concentration of 50 p.p.m. in the field experiments, in case any undetectable deleterious effects might have been caused by the higher concentration.

TABLE 18

Condition of _Corophium_ during the course of the experiment to determine the optimum dye concentration for field experiments in _Corophium_ movement.

Days after staining	Concentration of Neutral Red (p.p.m.)		
	10	50	100
1	Very lightly stained	Heavily stained thorax and abdomen with bright pink appendages	Heavily stained thorax and abdomen with bright pink appendages
2	Very lightly stained	Heavily stained thorax and abdomen with bright pink appendages (1 animal dead on sediment surface)	Heavily stained thorax and abdomen with bright pink appendages
3	Very lightly stained	Heavily stained thorax and abdomen with bright pink appendages	Heavily stained thorax and abdomen with bright pink appendages
4 (_Corophium_ sieved from mud)	15 alive (5 - unstained, 10 - traces of stain just visible)	14 alive (all heavily stained)	14 alive (all heavily stained)

b. Field experiments: -

Field experiments were performed at Site B in the region of transect BM (Fig. 2). A square, bottomless, plywood enclosure (Fig. 39) was used in the first field experiments. At high water the enclosure was placed in position on the mud surface and the height of the sea noted on the scale inside the enclosure. Sufficient neutral red solution was then added to produce a concentration of 50 p.p.m. The enclosure was then left in position until the tide had receded beyond it. There was negligible leakage of dye through the vertical joints of the enclosure. Leakage did occur beneath the bottom of the enclosure since water levels inside and outside both fell at the same rate. However, dye that did leak was rapidly dispersed by the tide and only mud within the enclosure was stained.

The first area stained (X) was situated approximately 25 m downshore from MHWS and left for seventeen tides. The second area stained (Y) was situated approximately 60 m downshore and left for three tides. Sampling was performed after seventeen tides at X, and after one and three tides at Y. In each case samples measuring 10 cm x 10 cm x 10 cm were collected at varying distances from the stained area and washed through a 20 mesh per inch sieve. The numbers of stained and unstained *Corophium* in each sample were noted. Results from area Y are given in Fig. 40 and from area X in Fig. 41.

The distribution of samples collected in the above method was restricted to four directions only, at right angles to each other. A second investigation was performed using a hollow aluminium cylinder 30 cm in height and enclosing 300 cm^2 of mud, thus enabling samples to be taken in six directions from the stained

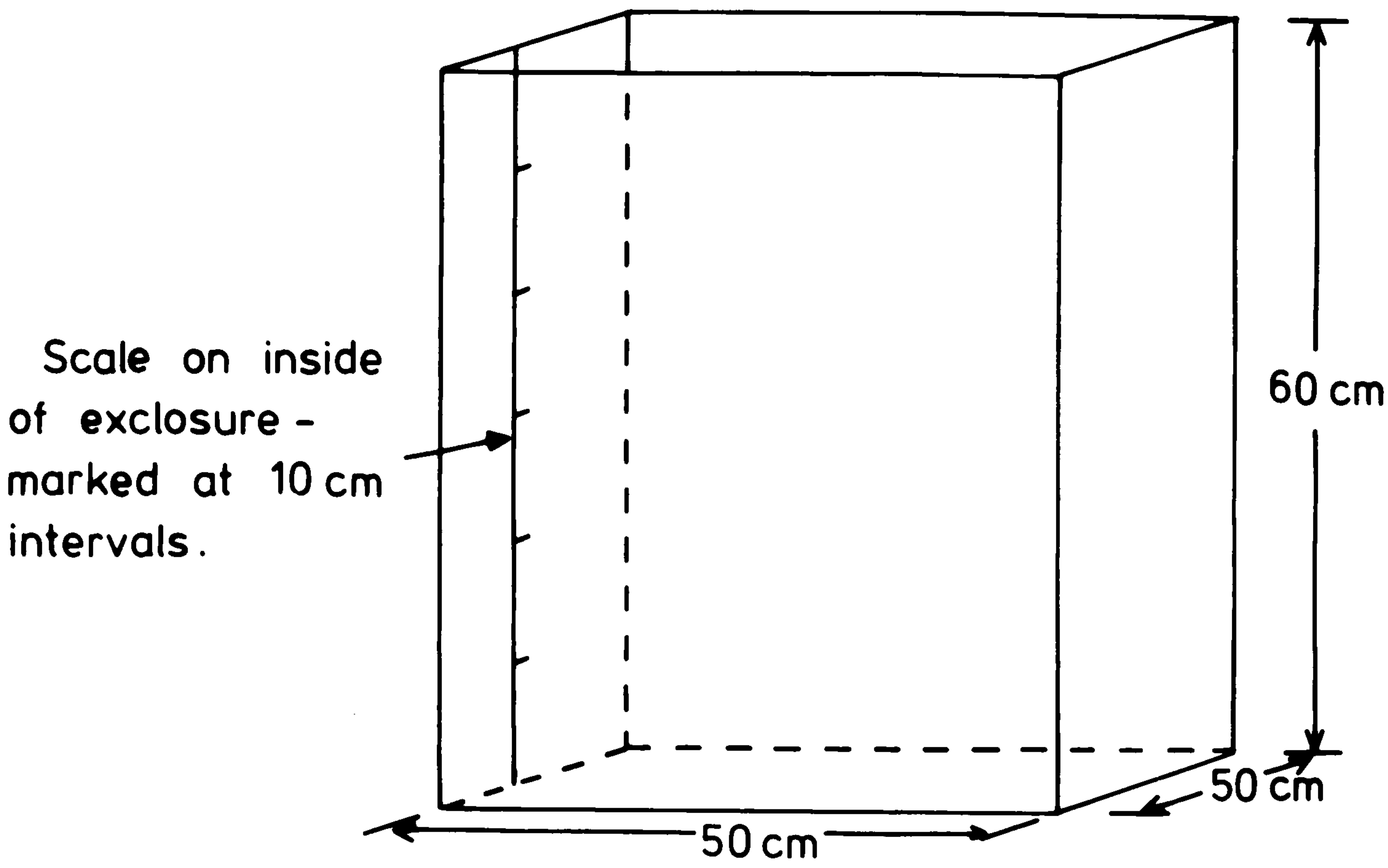


Fig. 39. Plywood enclosure for staining of *Corophium volutator*.

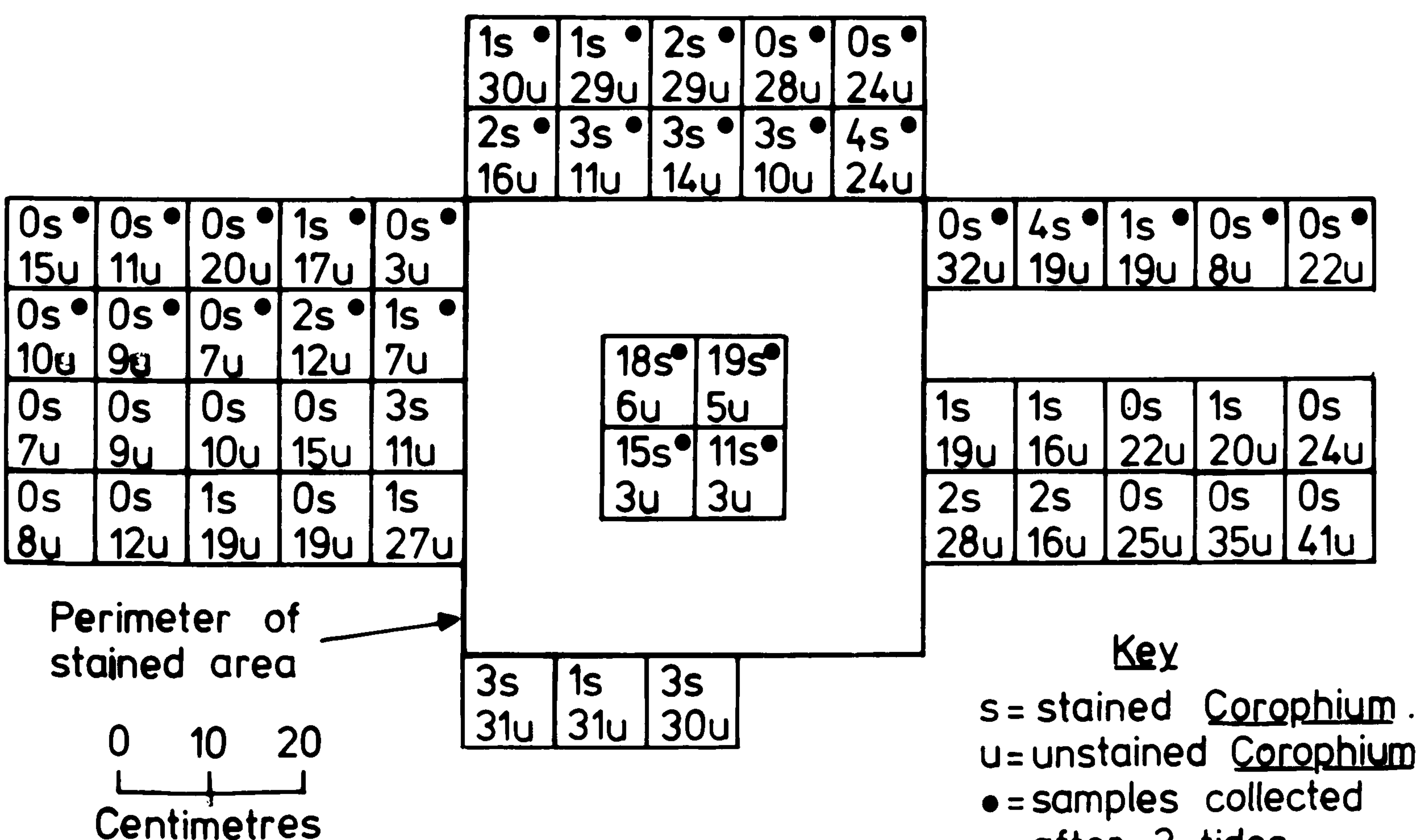


Fig. 40. Numbers of *Corophium volutator* from within and around Area Y after 1 and 3 tides.

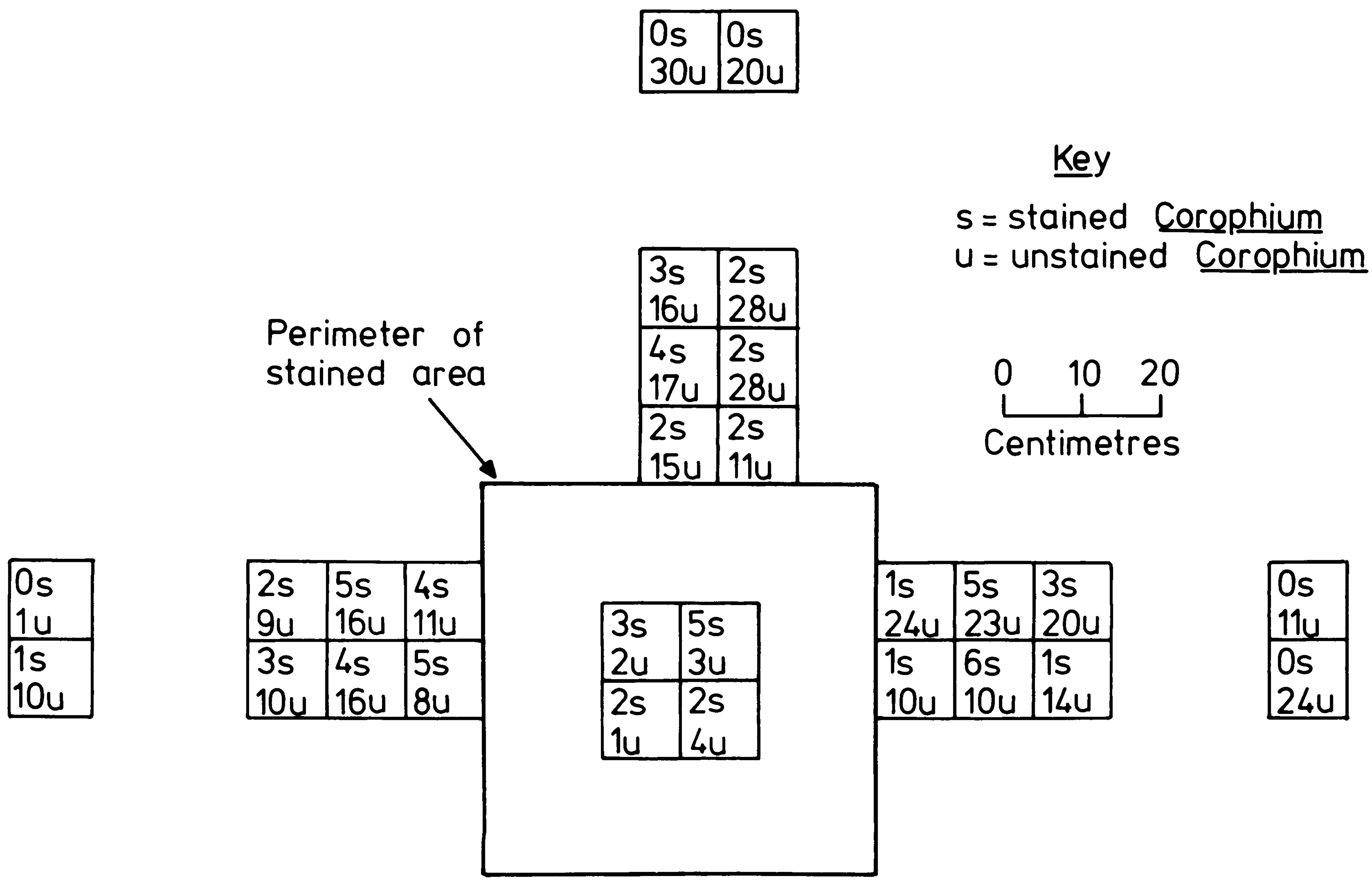


Fig. 41. Numbers of *Corophium volutator* from within and around Area X after 17 tides.

area (Z). The cylinder was placed approximately 40 m downshore of MHWS and staining of the area was as described for X and Y. Samples were collected after one tide. The results are given in Fig. 42.

A mean density for stained Corophium was calculated for each successive area beyond the perimeter of the stained area (i.e. 1st area - up to 10 cm from perimeter; 2nd area - up to 20 cm from perimeter; 3rd area - up to 30 cm from perimeter; etc.). The size of these areas was calculated as shown in Fig. 43. An estimation was then made of the total number of stained Corophium in each of the areas beyond the perimeter of the stained area. The mean density of stained Corophium within the stained area was then calculated from the four samples collected in areas X and Y and the one from area Z, and used to calculate the total number remaining within the area. This figure, summed with the estimated total of stained Corophium outside, gave an estimate of the total number of Corophium originally stained. The numbers of stained Corophium in each of the surrounding areas were then converted to percentages of the estimated total originally stained. The total density of Corophium (stained and unstained) within each area was also calculated and hence an estimate was made of the total number remaining within the area at the end of the experiment. By comparing this total with that at the beginning of the experiment, any net movement in or out of the stained area was detected.

The lengths of all individuals collected (stained individuals inside and outside each area, and unstained individuals from inside each area) were measured in the laboratory.

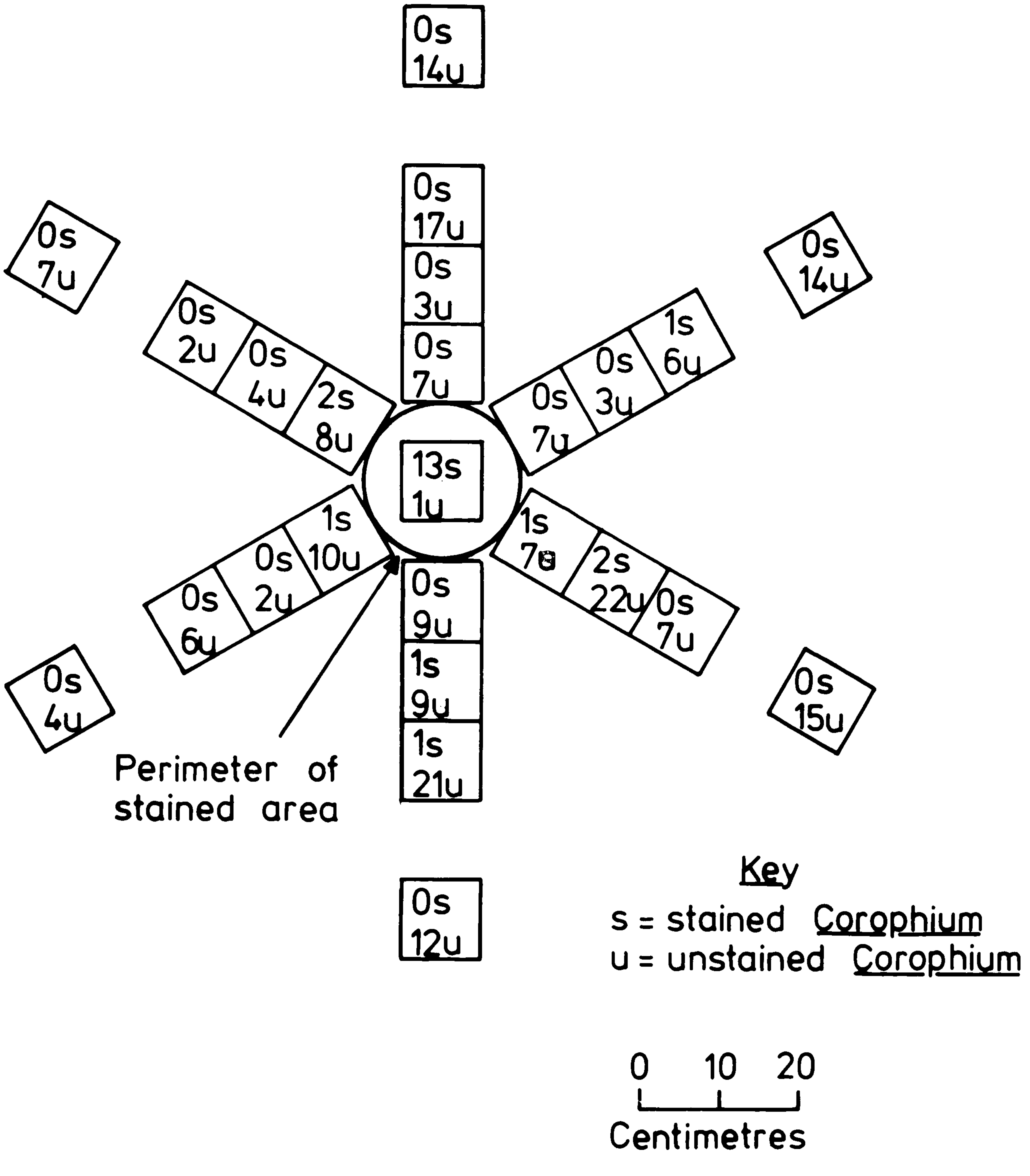
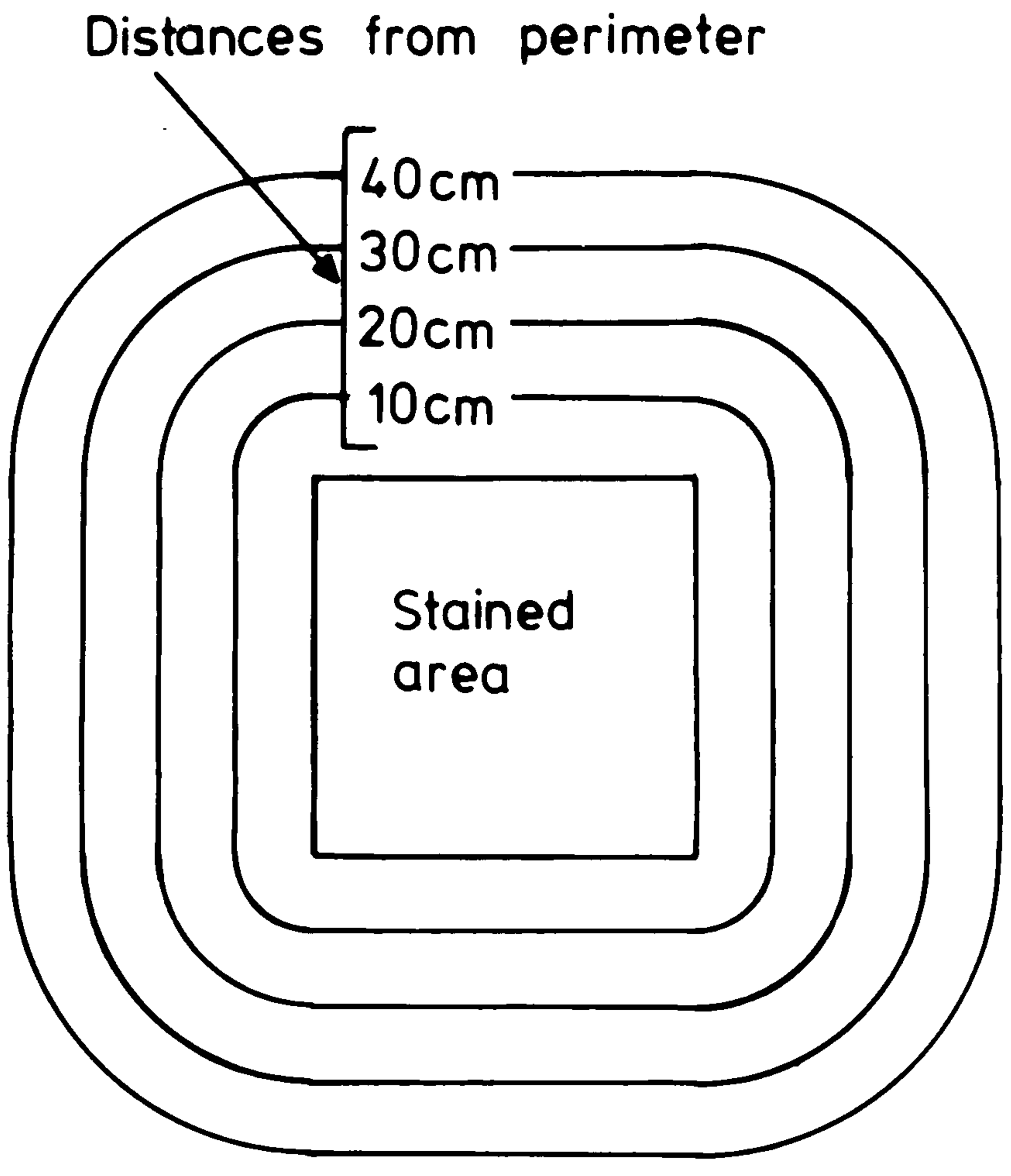


Fig. 42. Numbers of <u>Corophium volutator</u> from within and around Area Z after 1 tide.

a.



Area between n and n + 10 cm from perimeter of stained area

$= 2000 + \pi[(n+10)^2 - n^2]\,cm^2$

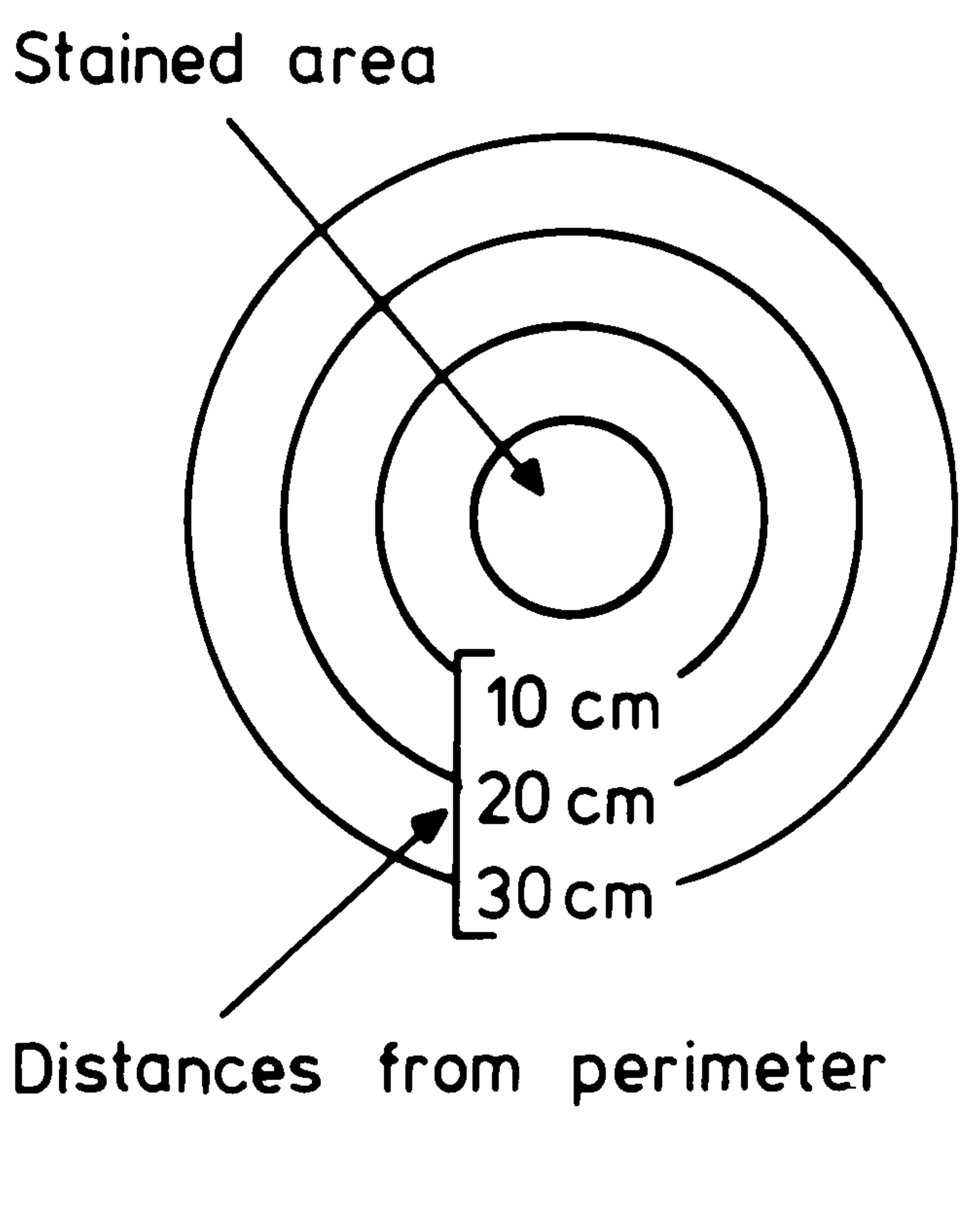
e.g. Area between 10 and 20 cm

$= 2000 + \pi(20^2 - 10^2)$

$= 2000 + 942{\cdot}6$

$= 2942{\cdot}6\ cm^2$.

b.



Radius of stained area $= 9{\cdot}771$ cm

Area between n and n + 10 cm from perimeter of stained area

$= \pi[(19{\cdot}771 + n)^2 - (9{\cdot}771 + n)^2]\,cm^2$

e.g. Area between 0 and 10 cm

$= \pi[(19{\cdot}771)^2 - (9{\cdot}771)^2]$

$= \pi\ 295{\cdot}33$

$= 927{\cdot}6\ cm^2$.

Fig. 43. Determination of successive areas beyond the perimeter of the stained areas a. X and Y, and b. Z.

Results (Tables 19 and 20): -

In all three experiments (X, Y and Z) stained _Corophium_ were found outside the stained area, indicating that movement had taken place. In area Y there was little difference between _Corophium_ distribution after one and three tides. Approximately 20% of the estimated total number of _Corophium_ stained had moved from the area, most of these being found within 20 cm of the perimeter. In area X, which was sampled after seventeen tides, approximately 80% of the stained animals were found outside the stained area, most of these occurring between 10 cm and 20 cm from the perimeter. Area Z had a larger percentage (approximately 40%) occurring outside the stained area after one tide than area Y. However, if the _Corophium_ all moved at about the same rate this would be expected, since area Z was smaller than area Y, and thus a _Corophium_ moving 20 cm from the centre of Y would still be within the stained area, whereas one moving 20 cm from the centre of area Z would be outside the stained area. The amount of movement detected in these experiments would be sufficient to explain the increase in density inside the exclosure by a net movement of individuals into it.

In both areas X and Z (but not area Y) noticeably fewer _Corophium_ were estimated to be present after the experiment than before, thus indicating a net movement away from the stained area. It might be argued that dyed sediment is unfavourable to _Corophium_ and they therefore try to avoid it by moving away. If this were so then a large proportion of the movement demonstrated in these experiments could have been induced by the experiment itself and not be a natural feature of _Corophium_ behaviour, However, in the preliminary experi-

TABLE 19

Results of field experiment in Corophium volutator movement at Site B. Areas are defined by their distance (in cm) from the perimeter of the stained area.

Area	Size of area (cm^2)		Mean density of stained Corophium (Numbers per 100 cm^2 ± 2 S.E.s)				Estimated total number of stained Corophium within area			
	X and Y	Z	X (17 tides)	Y (1 tide)	Y (3 tides)	Z (1 tide)	X (17 tides)	Y (1 tide)	Y (3 tides)	Z (1 tide)
Stained area	2500	300	3.00 ± 1.41	-	15.75 ± 3.61	13.00	75.00 ± 35.34	-	393.75 ± 90.14	39.00
Up to 10 cm	2314.2	927.6	2.33 ± 1.12	2.29 ± 0.72	2.00 ± 1.07	0.67 ± 0.67	53.92 ± 25.96	52.89 ± 16.62	46.27 ± 24.76	6.19 ± 6.18
Between 10 and 20 cm	2942.6	1856.4	4.33 ± 1.10	0.75 ± 0.96	1.38 ± 0.92	0.50 ± 0.68	127.50 ± 32.41	22.07 ± 28.19	40.46 ± 27.13	9.28 ± 12.68
Between 20 and 30 cm	3571.0	3115.6	2.33 ± 0.68	0.25 ± 0.50	0.33 ± 0.67	0.33 ± 0.39	83.22 ± 24.14	8.93 ± 17.85	11.79 ± 23.79	10.38 ± 12.18
Between 30 and 40 cm	4199.4	4666.4	-	0.25 ± 0.50	0	-	-	8.93 ± 17.85	0	-
Between 40 and 50 cm	4827.8	6553.6	-	0	0	0	-	0	0	0
Between 50 and 60 cm	5456.2		0.17 ± 1.41				9.06 ± 20.18			
Estimated total number of stained Corophium at beginning of experiment =							348.7		492.3	65.0
Estimated total number of Corophium present in stained area at end of experiment =							137.5		500.0	42.0

TABLE 20

Distribution of Corophium volutator (as a percentage of those originally stained) during the course of experiments in Corophium movement at Site B.

Distance from stained area	Area X (17 tides)	Area Y (1 tide)	Area Y (3 tides)	Area Z (1 tide)
Stained area	21.52	81.16	79.98	60.23
Up to 10 cm	15.46 ± 7.44	10.74 ± 3.38	9.40 ± 5.03	9.52 ± 9.51
Between 10 cm and 20 cm	36.56 ± 9.29	4.48 ± 5.73	8.22 ± 5.51	14.28 ± 19.51
Between 20 cm and 30 cm	23.86 ± 6.92	1.81 ± 3.62	2.40 ± 4.83	15.97 ± 18.74
Between 30 cm and 40 cm	-	1.81 ± 3.62	0	-
Between 40 cm and 50 cm	-	0	0	0
Between 50 cm and 60 cm	2.60 ± 5.79	-	-	-

ment to determine the optimum dye concentration, Corophium burrowed quickly into the dyed sediment. In addition, if stained sediment was unfavourable to Corophium, it is unlikely that as many as 80% of those stained would have remained within the stained area for three tides.

No evidence was found from the mean lengths of Corophium (Table 21) that larger animals moved further than smaller ones.

TABLE 21

Mean lengths ($\pm$ 2 S.E.s) of Corophium volutator (in mm) from field experiments in Corophium movement at Site B. Samples sizes (n) are given. The mean lengths of stained and unstained Corophium within the stained area Y were compared and t was found to be 1.895 (P > 0.05)

<table>
<tr><th rowspan="2"></th><th colspan="2">Inside stained area</th><th colspan="3">Outside stained area</th></tr>
<tr><th>Stained Corophium</th><th>Unstained Corophium</th><th colspan="3">Stained Corophium</th></tr>
<tr><td>Area X
(after 17 tides)</td><td>6.75 ± 0.33
n = 11</td><td>6.37 ± 0.49
n = 14</td><td colspan="3">6.57 ± 0.25
n = 50</td></tr>
<tr><td>Area Y
(after 1 tide)</td><td>-</td><td>-</td><td colspan="3">6.99 ± 0.22
n = 21</td></tr>
<tr><td>Area Y
(after 3 tides)</td><td>6.99 ± 0.22
n = 63</td><td>7.32 ± 0.28
n = 16</td><td colspan="3">6.98 ± 0.23
n = 29</td></tr>
<tr><td></td><td></td><td></td><td colspan="3">Distance from Area Z</td></tr>
<tr><td></td><td></td><td></td><td>10 cm</td><td>20 cm</td><td>30 cm</td></tr>
<tr><td>Area Z
(after 1 tide)</td><td>6.51 ± 0.58
n = 15</td><td>-</td><td>6.74 ± 0.39
n = 4</td><td>6.92 ± 1.07
n = 3</td><td>6.62
n = 2</td></tr>
</table>

CHAPTER 6. DETAILED STUDY OF *HYDROBIA ULVAE*

i. Mean sizes of animals inside and outside *Spartina*.

Measurements were made of all animals collected in June and December 1973 at Site B and August and December 1973 at Site E (see Chapter 4. iii. p 42). The length of each animal was measured from the base of its shell to the apex. (Measurements were not taken from animals with broken apices).

Results: -

Histograms of size distribution were prepared for all animals taken within, and all taken outside, the *Spartina*, in summer and winter at Site B (Fig. 44) and Site E (Fig. 45). As may be seen, all distributions were unimodal and not markedly skewed. Hence t-tests between means are appropriate.

Mean lengths ($\pm$ 2 standard errors) were calculated for each sample at Site B (Table 22) and Site E (Table 23). Unlike *Corophium*, mean lengths of *Hydrobia* from individual samples within *Spartina* were not invariably greater than those from outside the *Spartina* at either of the two Sites in summer and winter. Therefore pairs of individual samples were not compared using t-tests. Nevertheless, at Site B in June, the three largest mean lengths occurred in Transect BS, two of these occurring within *Spartina* (BS 90 and BS 120). In Transect BC the two largest mean lengths were both found at *Spartina* stations (BC 90 and BC 120). In December, animals with the largest mean length were found within *Spartina* (BS 90). At Site E comparisons between transects are irrelevant since only small numbers of *Hydrobia* were obtained from transect EM (8 in August and 11 in December). How-

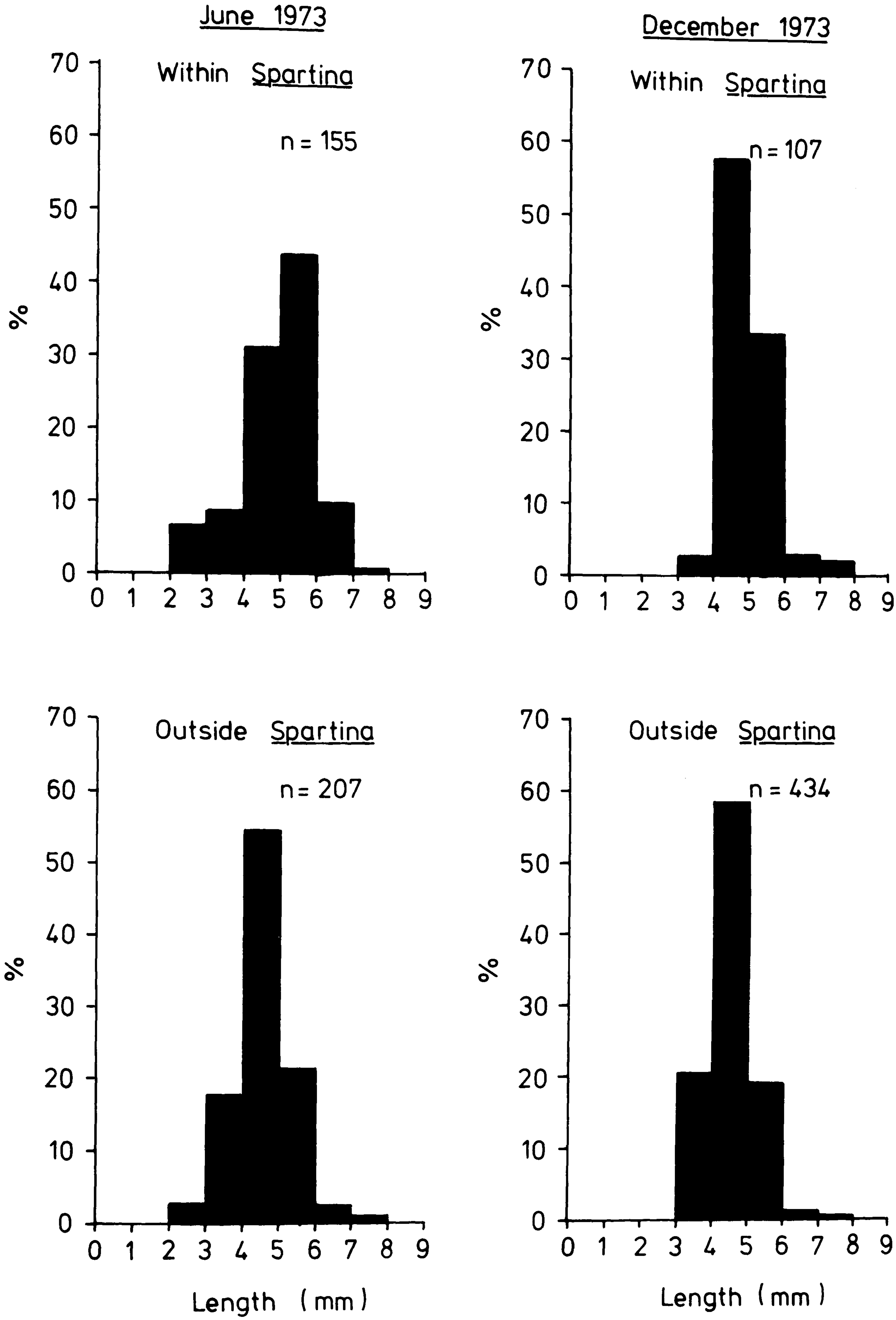


Fig. 44. Histograms of size distribution for *Hydrobia ulvae* at Site B.

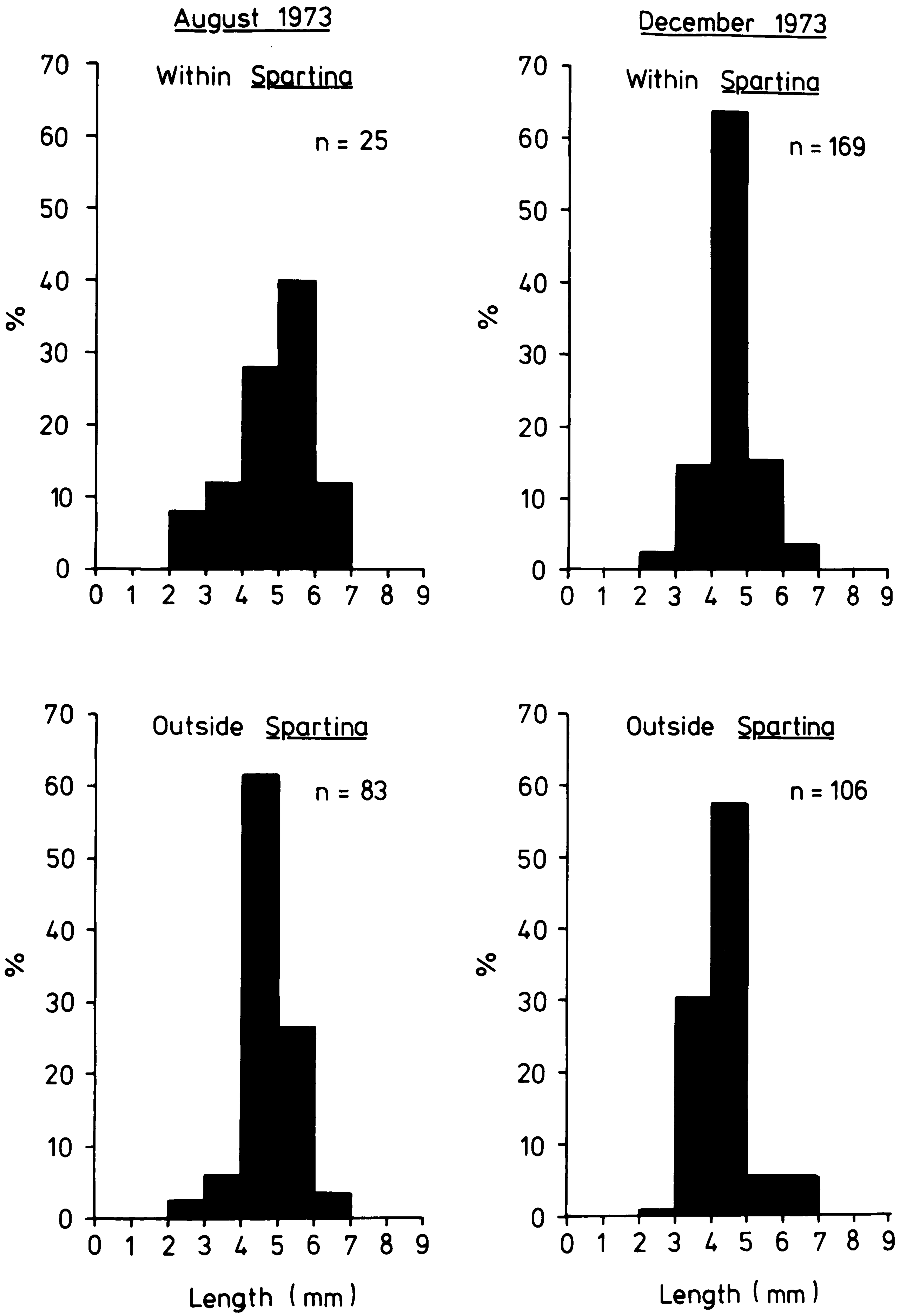


Fig. 45. Histograms of size distribution for *Hydrobia ulvae* at Site E.

ever, in both August and December the largest mean length occurred within Spartina at station ES 60.

An overall mean length of Hydrobia from within Spartina was calculated for each site in both summer and winter. Similar calculations were made for Hydrobia outside Spartina (Tables 22 and 23). At Site B Hydrobia within Spartina were significantly longer than those outside in both June ($t = 3.864$, $P < 0.001$) and December ($t = 5.202$, $P < 0.001$). At Site E, no significant differences were found either in August ($t = 0.555$, $P > 0.1$) or December ($t = 1.928$, $P > 0.05$). However, the histograms show that at both Sites B (Fig. 44) and E (Fig. 45) relatively more Hydrobia above 5 mm in length were found inside the Spartina than outside.

ii. Mean dry weights of animals inside and outside Spartina.

All Hydrobia collected in December 1973 were sorted according to size class and transect. The small numbers of animals in some size classes made it impossible to divide the animals between those occurring inside and those occurring outside the Spartina, as with Corophium. Dry weights were determined as described for Corophium (see Chapter 5. ii. p 50). Before vacuum drying, the mineral content of the shells was removed by dissolving them in N/5 hydrochloric acid.

Results: -

Untransformed weights are given in Appendix 4 (p 141); weights plotted against lengths on a double logarithmic scale are shown for both sites B and E in Fig. 46. At Site B four of the dry weights from transect BS were greater than the corresponding ones from transect BM. The probability of this occurring by chance is 5 in 2^5 ($P = 0.16$) and hence not significant. At Site E the small

TABLE 22

Mean lengths ($\pm$ 2 S.E.s) of _Hydrobia ulvae_ (in mm) at Site B. Sample sizes (n) are given and those from within _Spartina_ are indicated by •.

	Transect	Distance from MHWS (m) 15	30	60	90	120	150	180	210
June 1973	BS	4.83 $\pm$ 0.67• n = 3	-•	-•	5.50 $\pm$ 0.33• n = 20	5.27 $\pm$ 0.23• n = 26	5.44 $\pm$ 0.44 n = 17		
	BC	-	-	4.50 $\pm$ 0.19 n = 27	5.06 $\pm$ 0.44• n = 16	5.18 $\pm$ 0.35• n = 34	4.50 $\pm$ 0.33• n = 9	4.39 $\pm$ 0.37• n = 44	4.73 $\pm$ 0.46 n = 13
	BM	-	4.67 $\pm$ 0.33 n = 6	4.27 $\pm$ 0.11 n = 27	4.85 $\pm$ 0.45 n = 17	4.33 $\pm$ 0.25 n = 41	4.37 $\pm$ 0.46 n = 23	4.67 $\pm$ 0.33 n = 12	4.45 $\pm$ 0.35 n = 26
December 1973	BS	-	-•	-•	5.17 $\pm$ 0.36• n = 18	-•	4.72 $\pm$ 0.22 n = 59		
	BC	-	4.83 $\pm$ 0.34 n = 3	-	4.93 $\pm$ 0.19• n = 60	-•	4.74 $\pm$ 0.16• n = 29	-•	4.61 $\pm$ 0.19 n = 44
	BM	-	4.29 $\pm$ 0.27 n = 33	-	4.31 $\pm$ 0.10 n = 185	-	4.87 $\pm$ 0.13 n = 68	-	4.81 $\pm$ 0.20 n = 42

Overall mean length of _Hydrobia_ from within _Spartina_ in June 1973 = 4.94 $\pm$ 0.16
" " " " " " outside " " " " = 4.55 $\pm$ 0.12
" " " " " " within " December 1973 = 4.92 $\pm$ 0.13
" " " " " " outside " " " = 4.54 $\pm$ 0.07

TABLE 23

Mean lengths ($\pm$ 2 S.E.s) of *Hydrobia ulvae* (in mm) at Site E.

Sample sizes (n) are given and those from within *Spartina* are indicated by *.

	Transects	Distance from MHWS (m) 30	60	90	120	150	180	210
August 1973	EM	-	-	4.00 n = 2	-	4.50 n = 1	-	4.70 $\pm$ 0.74 n = 5
	ES	5.00 $\pm$ 0.86 n = 6	5.25 $\pm$ 0.26* n = 12	4.50 $\pm$ 0.79* n = 13	5.21 $\pm$ 0.58 n = 7	4.72 $\pm$ 0.17 n = 45	4.75 $\pm$ 0.96 n = 4	4.50 $\pm$ 0.32 n = 13
December 1973	EM	4.5 n = 1	-	4.00 n = 2	-	-	-	4.30 $\pm$ 0.75 n = 5
	ES	4.33 $\pm$ 0.96 n = 6	4.61 $\pm$ 0.17* n = 88	4.44 $\pm$ 0.15* n = 81	-	4.30 $\pm$ 0.40 n = 5	-	4.19 $\pm$ 0.12 n = 78

Overall mean length of *Hydrobia* from within *Spartina* in August 1973 = 4.86 $\pm$ 0.45
" " " " " " outside " " " " = 4.55 $\pm$ 0.16
" " " " " " within " December 1973 = 4.53 $\pm$ 0.11
" " " " " " outside " " " = 4.35 $\pm$ 0.15

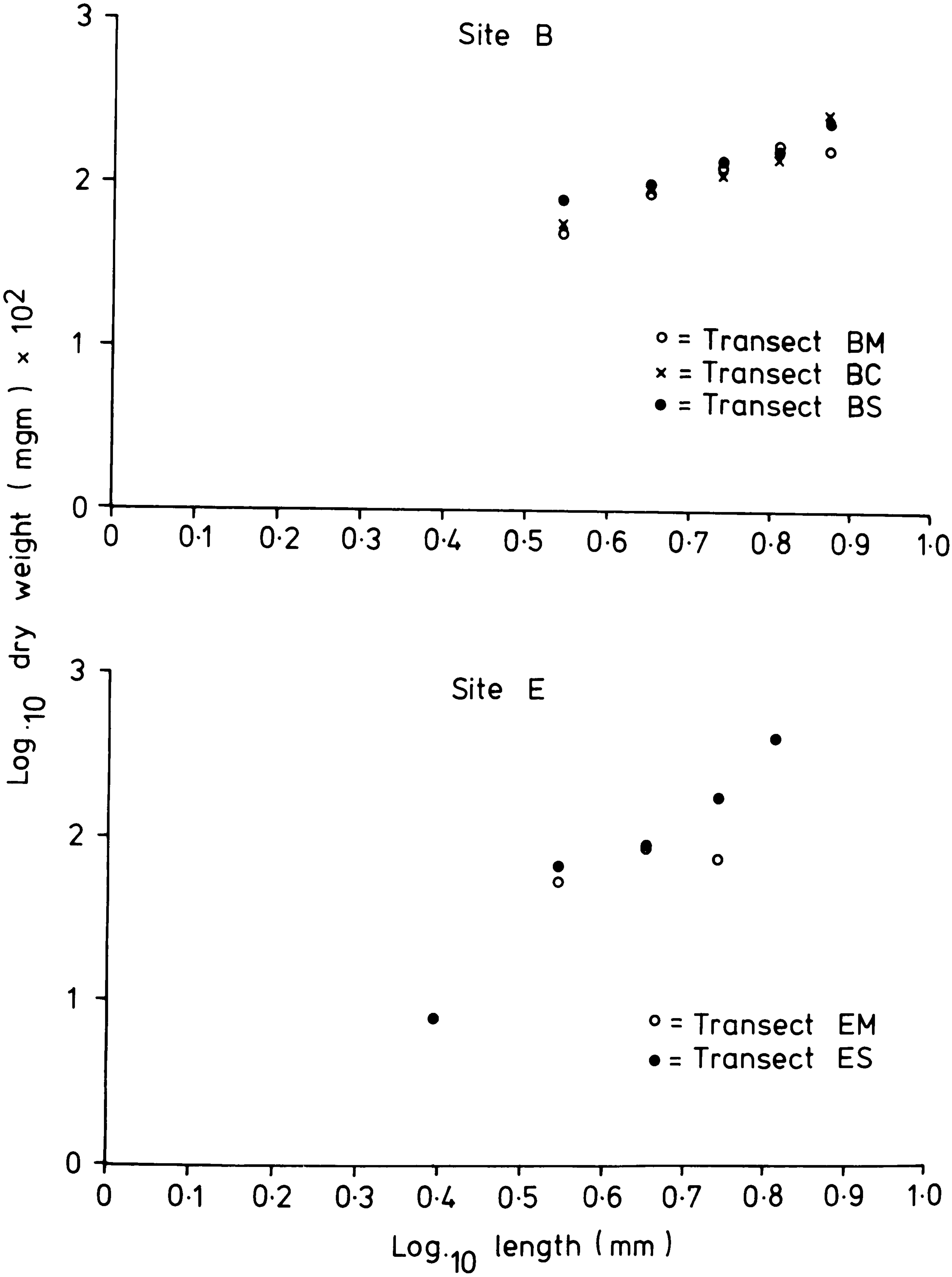


Fig. 46. Log. weights of Hydrobia ulvae for December 1973 plotted against log. lengths at Sites B and E.

numbers of Hydrobia in transect EM provide only three points on the graph for comparison with transect ES. It was concluded that at both Sites B and E there was no real differences between dry weights of Hydrobia from transects through Spartina and across open mud.

iii. Habitat selection by Hydrobia

Hydrobia densities in relation to silt/clay content of the sediment were investigated in Summer 1973 at Sites B and E (Fig. 47). Results from stations at MHWS, which is at or above the upshore limit of Hydrobia distribution (Green 1968) have been omitted. At Site B (Fig. 47a) Hydrobia density tended to rise with increasing silt content up to approximately 50% silt/clay. Above this the density dropped until above 85% silt/clay there were few or no Hydrobia. At Site E (Fig. 47b) all silt/clay contents were below 30%. The relationship shown is similar to the left half of Fig. 47a, and confirms the increase in Hydrobia density with increasing silt/clay content.

iv. Winter predation of Hydrobia: Exclosure experiments

Exclosures of the type described in Chapter 5. v. (p 55) were used in a preliminary study of Hydrobia predation during winter 1972/73 and in a further study during winter 1973/74.

a. Preliminary study - 1972/73:

Exclosures were placed in each of the two areas used for bird observations (Sites B and W - Figs. 2 and 4) to provide results comparable with those obtained from direct observation of bird feeding behaviour. The Site B exclosure was positioned approximately 110 m downshore from MHWS along transect BM on 20/9/72. The Site W exclos-

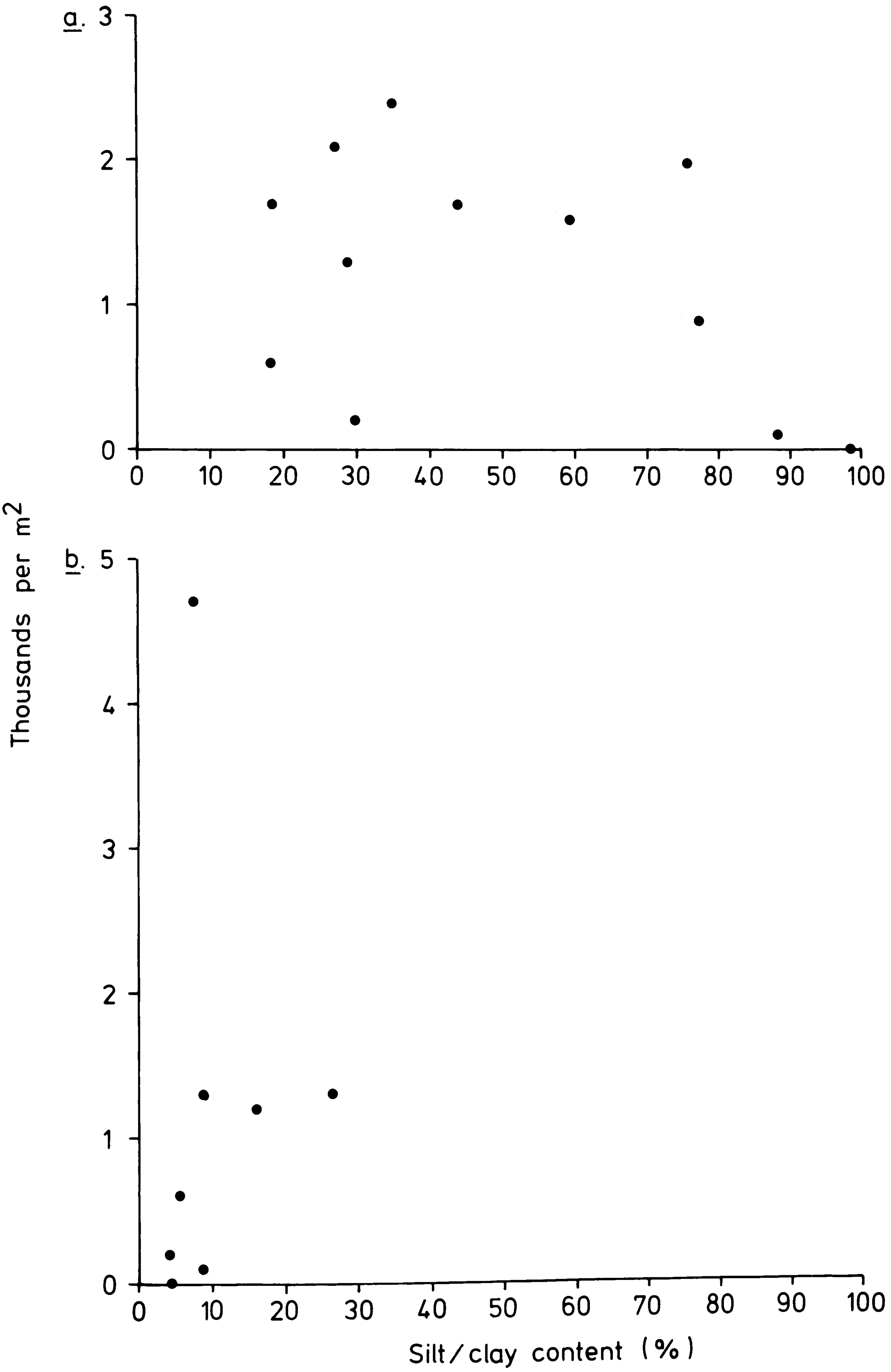


Fig. 47. Density of Hydrobia ulvae plotted against silt/clay content at a. Site B and b. Site E

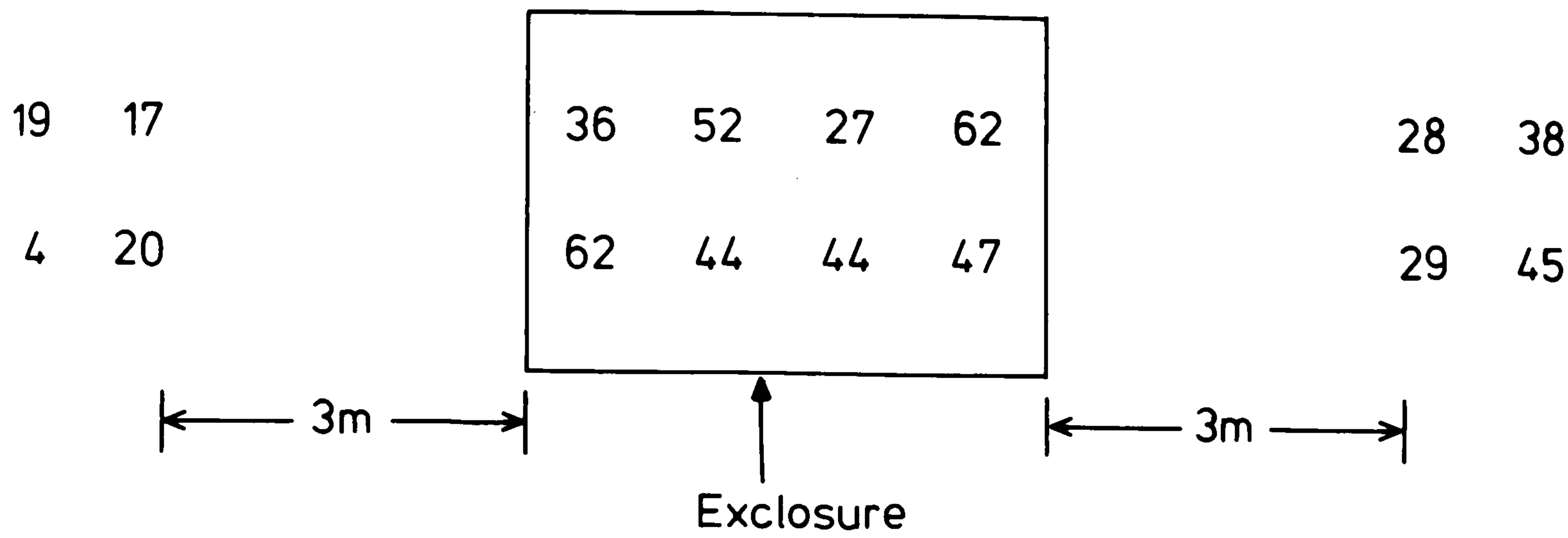
ure was positioned approximately 190 m downshore from MHWS on 16/10/72. No samples were taken at the time of positioning the exclosures. The Site B exclosure was removed on 11/5/73 and eight 10 cm x 10 cm x 10 cm mud samples taken from within the area of the exclosure and eight from outside. The Site W exclosure was removed on 9/5/73 and 16 samples taken, as at Site B.

Results: -

The numbers of Hydrobia in each sample associated with the two exclosures are shown in Fig. 48, together with mean densities. At Site B in May the density of Hydrobia within the exclosure was significantly higher than outside ($t = 3.27$, $P < 0.01$). At Site W the difference was not significant ($t = 0.477$, $P > 0.1$). Filamentous green alga was present within the Site B exclosure although no measurements were made of its abundance. If predation outside the Site B exclosure was solely responsible for the difference in densities then approximately 2,000 Hydrobia per m^2 (20 million per ha) must have been taken during the time the exclosure was in position. (cf. Ch.7.iv. p 97 . The Redshank mean daily predation rate per ha at Site B in 1973/74 suggests that approximately 4·3 million small food items were taken per ha by Redshank during the time the 1972/73 exclosure was in position, i.e. 233 days.) Alternatively, or additionally, the difference in densities could have been caused by a net movement of Hydrobia into the exclosure.

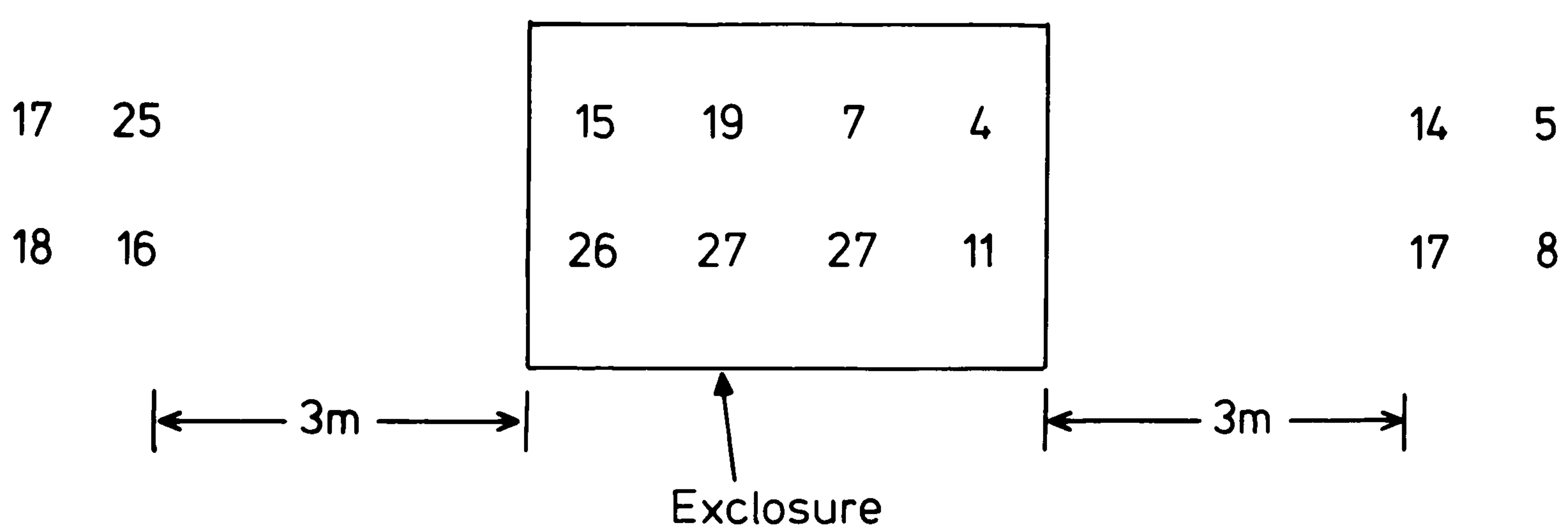
At both Sites B and W no significant differences were found between the mean lengths of Hydrobia inside and outside the exclosures (Figs. 49 and 50).

a.



Spring mean density inside exclosure = 4675 ± 908 per m^2
Spring mean density outside exclosure = 2500 ± 972 per m^2

b.



Spring mean density inside exclosure = 1700 ± 696 per m^2
Spring mean density outside exclosure = 1500 ± 466 per m^2

Fig. 48. Results of *Hydrobia ulvae* exclosure experiments in 1972/73 at a. Site B and b. Site W.

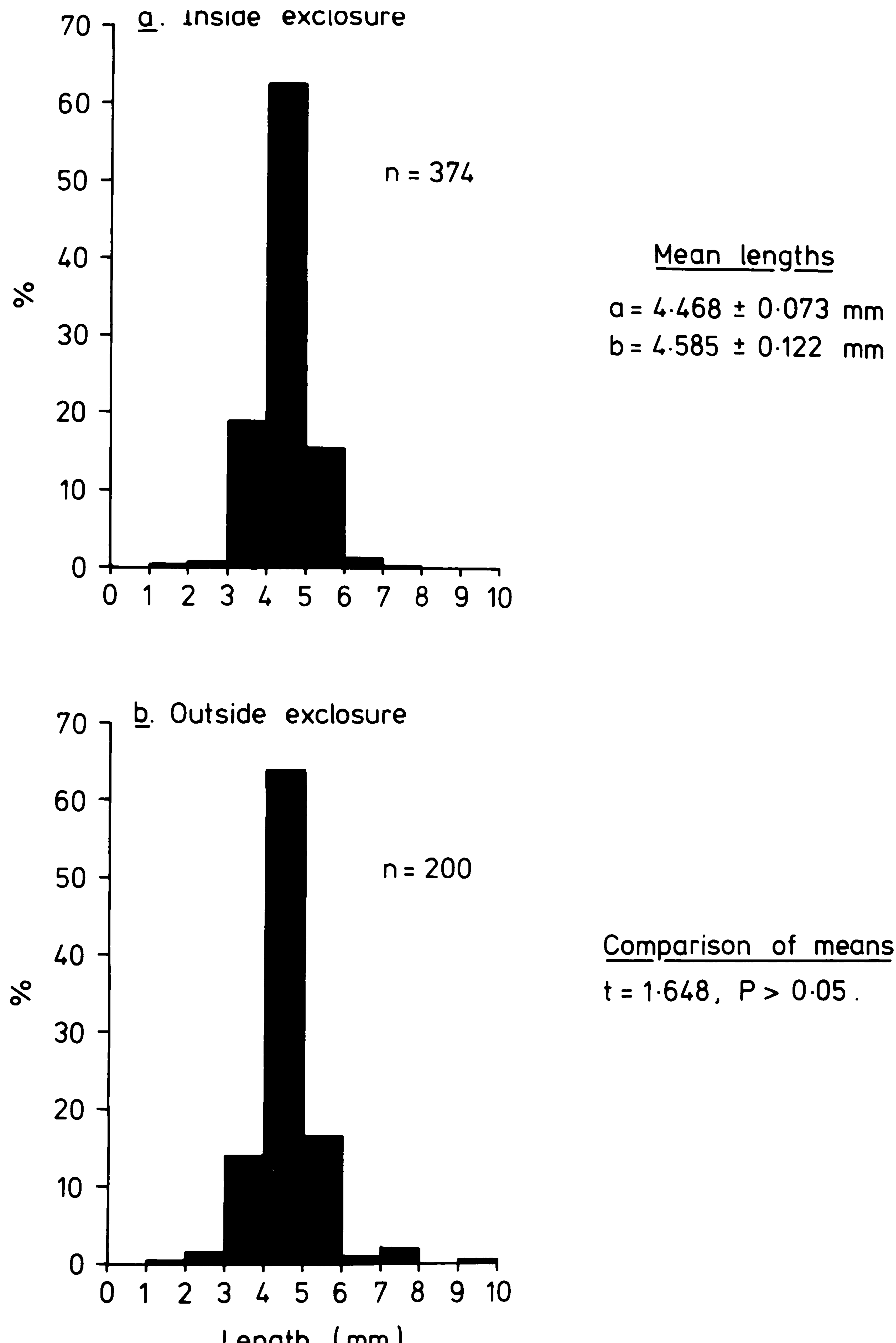


Fig. 49. Histograms of size distribution for Hydrobia ulvae from the exclosure experiment at Site B in 1972/73.

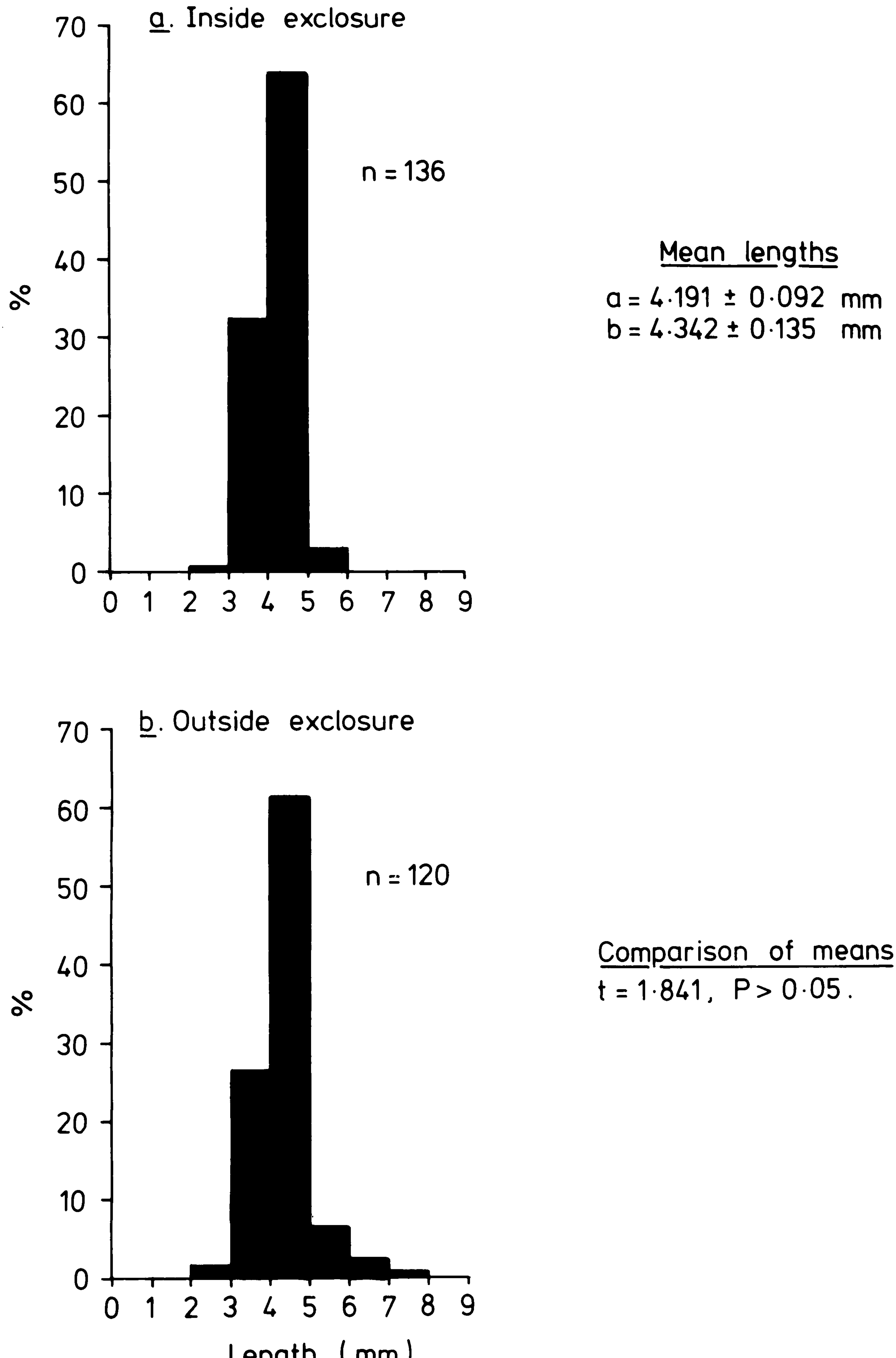


Fig. 50. Histograms of size distribution for Hydrobia ulvae from the exclosure experiment at Site W in 1972/73.

b. 1973/74 study: -

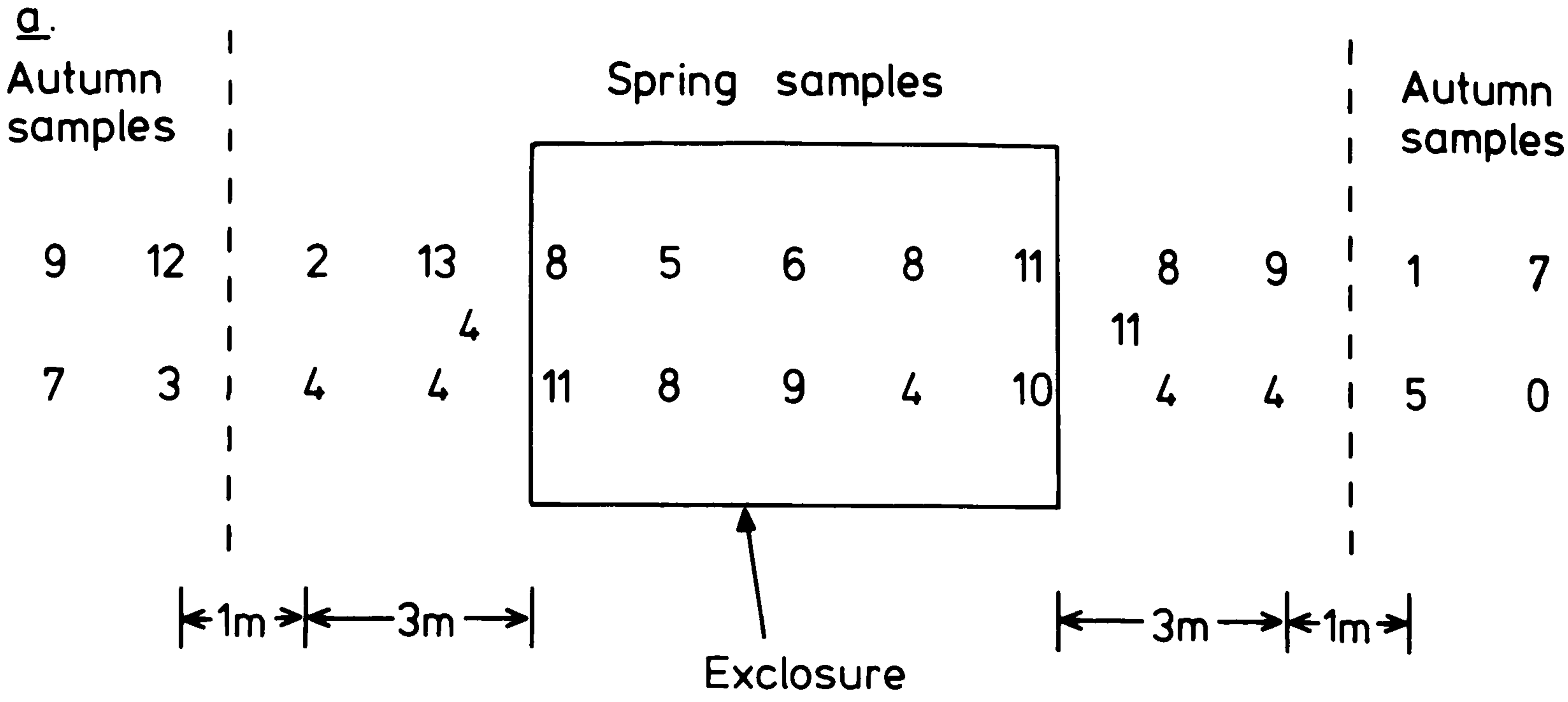
In 1973/74 exclosures were restricted to Site B to compare predation inside and outside areas of *Spartina*. In addition to the exclosure used to study predation of *Corophium* on transect BM (Ch. 5. v. p 55) another exclosure was positioned approximately 110 m downshore from MHWS on transect BS on 29/10/73. The exclosure on transect BS was removed on 8/4/74. Autumn and Spring densities of *Hydrobia* were determined at and near exclosures as described in Ch. 5. v.(p 55). In view of the possible net movement of *Hydrobia* into the Site W exclosure in 1972/73 sediment characteristics were compared inside and outside each of the two 1973/74 exclosures (as described in Ch. 5. v.) to check possible factors attracting *Hydrobia*.

Results: -

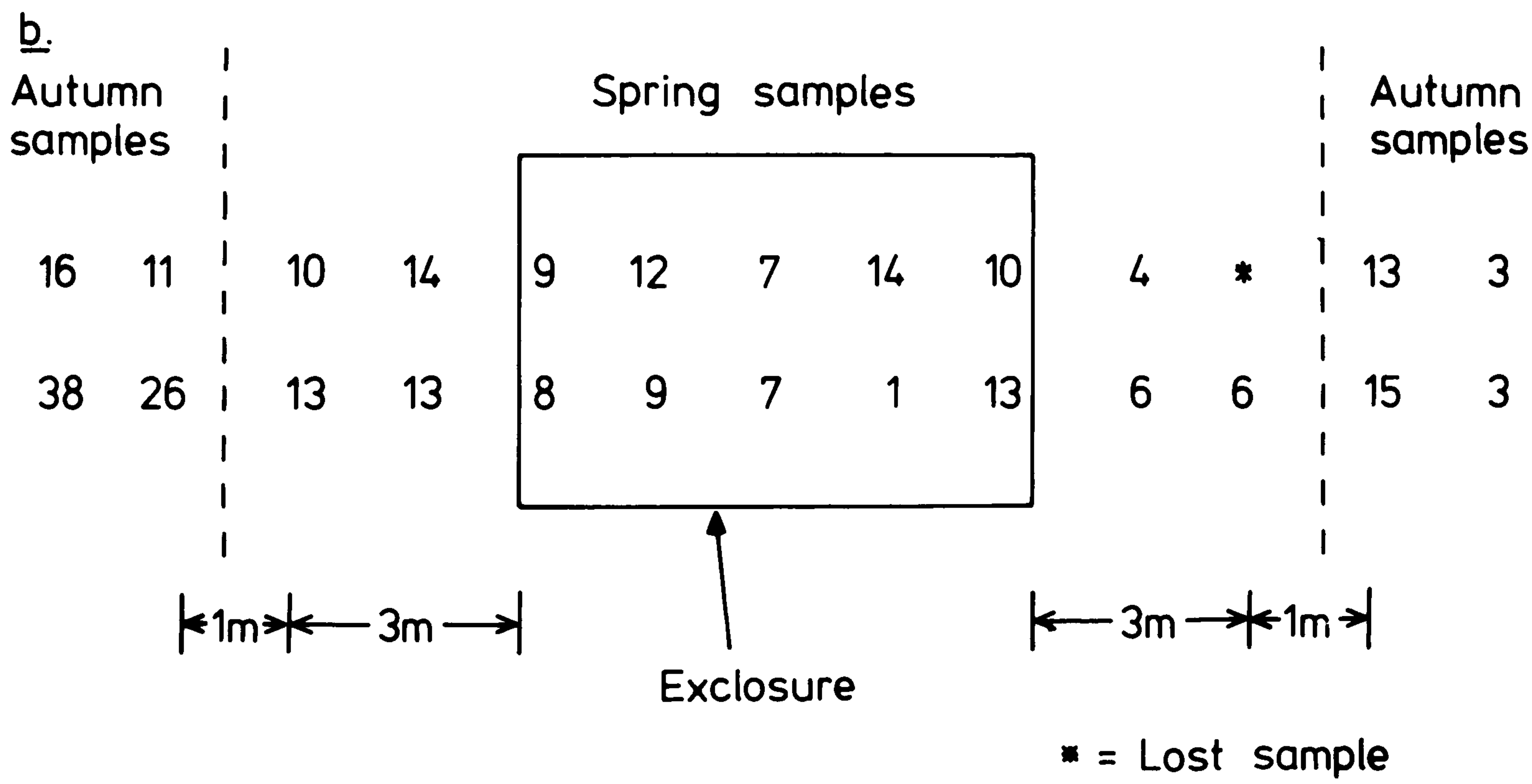
The numbers of *Hydrobia* in each sample associated with the two exclosures are given in Fig. 51 together with mean densities, which are compared in Table 24. Sediment characteristics are given in Table 25. In both exclosures there were no significant differences between Autumn and Spring densities, either inside or outside the exclosure (Table 24). Similarly there were no significant differences between mean lengths at either of the exclosures (Figs. 52 and 53). These results would have been expected if predation outside the exclosure had been negligible or if free movement of *Hydrobia* into and out of the exclosure had taken place.

v. Movement of *Hydrobia*

Wood (1972) compared the movement of marked *Hydrobia* on open mud with that near areas of *Enteromorpha*. A similar method was



Autumn mean density = 550 ± 288 per m^2
Spring mean density inside exclosure = 800 ± 152 per m^2
Spring mean density outside exclosure = 630 ± 233 per m^2



Autumn mean density = 1563 ± 826 per m^2
Spring mean density inside exclosure = 900 ± 235 per m^2
Spring mean density outside exclosure = 956 ± 309 per m^2

Fig. 51. Results of <u>Hydrobia ulvae</u> exclosure experiments on <u>a</u>. Transect BM and <u>b</u>. Transect BS in 1973/74.

TABLE 24

Comparison between *Hydrobia* densities associated with 1973/74 exclosure

	Comparison	*t*	*P*
Transect BS	Autumn and Spring inside exclosure	1.544	>0.1
	Autumn and Spring outside exclosure	1.378	>0.1
	Spring inside exclosure and Spring outside exclosure	0.286	>0.1
Transect BM	Autumn and Spring inside exclosure	1.537	>0.1
	Autumn and Spring outside exclosure	0.432	>0.1
	Spring inside exclosure and Spring outside exclosure	1.222	>0.1

TABLE 25

Sediment characteristics of Transect BS exclosure in 1973/74.

Sediment characteristic	Inside	Outside
Carbon content	6.35%	6.28%
Silt content	78.06%	78.41%
Median particle diameter	155 μ	155 μ

N.B. For sediment characteristics of Transect BM, see Table 17, p.60.

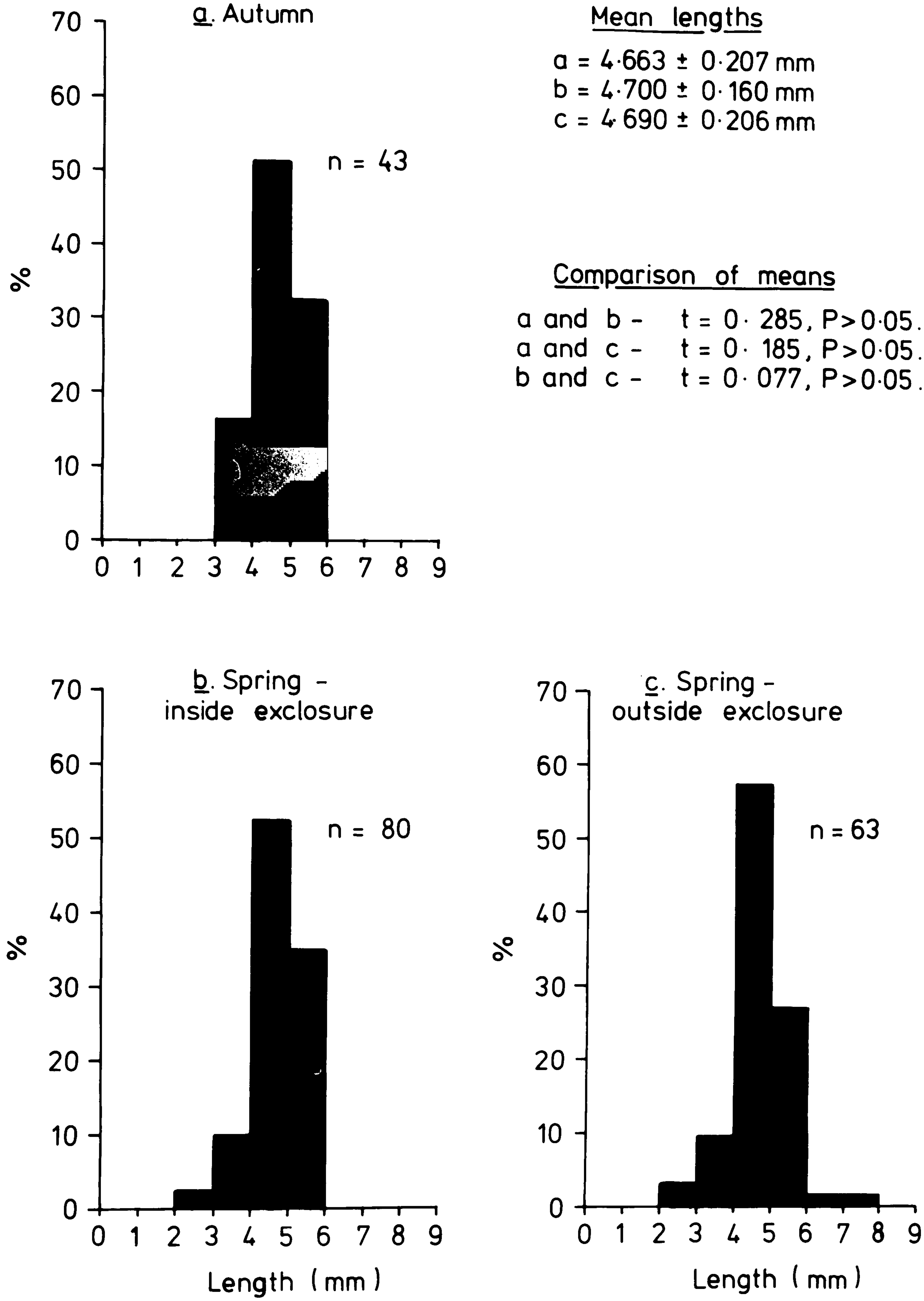


Fig. 52. Histograms of size distribution for <u>Hydrobia ulvae</u> from the exclosure experiment on Transect BM in 1973/74.

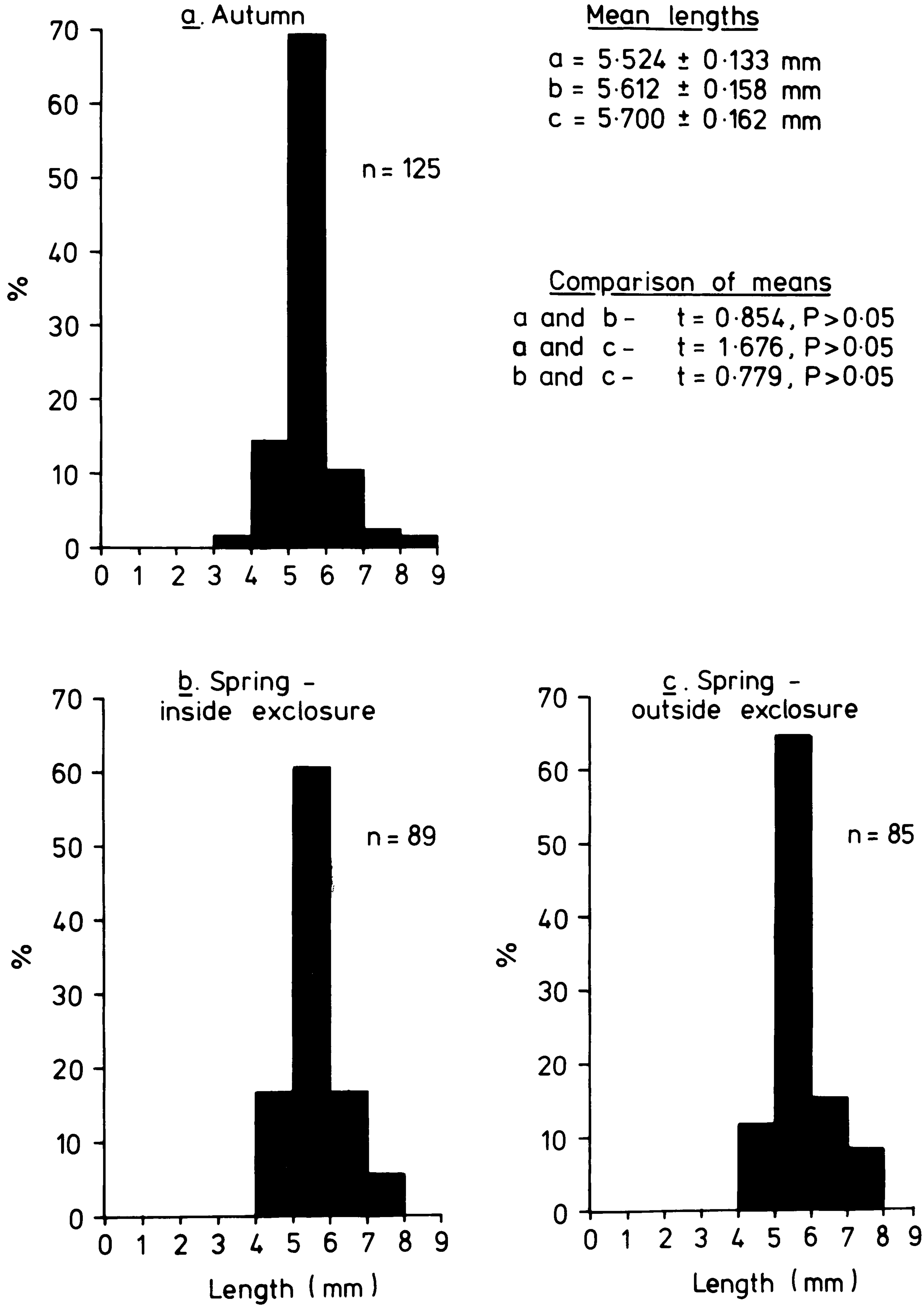


Fig. 53. Histograms of size distribution for Hydrobia ulvae from the exclosure experiment on Transect BS in 1973/74.

used a) to assess the importance of Hydrobia movement as a contributory factor in the exclosure results outlined above and b) to compare movement of Hydrobia inside and outside areas of Spartina.

Studies were made approximately 100 m downshore from MHWS on transect BS and at an equivalent level on transect BM. At each site a 50 cm x 50 cm quadrat was placed on the mud surface and Hydrobia removed from within the quadrat. All Hydrobia were washed in a sieve, dried on filter paper and marked with orange cellulose paint. A total of 97 animals from transect BS and 96 from transect BM were marked in this way. When the paint had dried the animals were wetted with seawater (to disperse trapped air bubbles) and replaced in their respective quadrats.

After 1, 2, 12 and 19 tides, the numbers of marked Hydrobia in each quadrat were noted. In addition the area immediately surrounding the quadrat was searched carefully for marked Hydrobia. The shortest distance between each of these and the perimeter of the quadrat was then noted.

Results: -

For each of the four observations at the two sites the mean distance moved by Hydrobia from the perimeter of the quadrat was calculated, using the total number of marked Hydrobia observed at that time. All Hydrobia remaining within the quadrat were treated as having moved 0 cm. In addition, for each observation and site, the percentage of marked Hydrobia which remained within the quadrat was calculated. The results are given in Figs. 54 and 55.

At first Hydrobia within the Spartina dispersed at a slower rate than those on open mud. However, between 12 and 19 tides

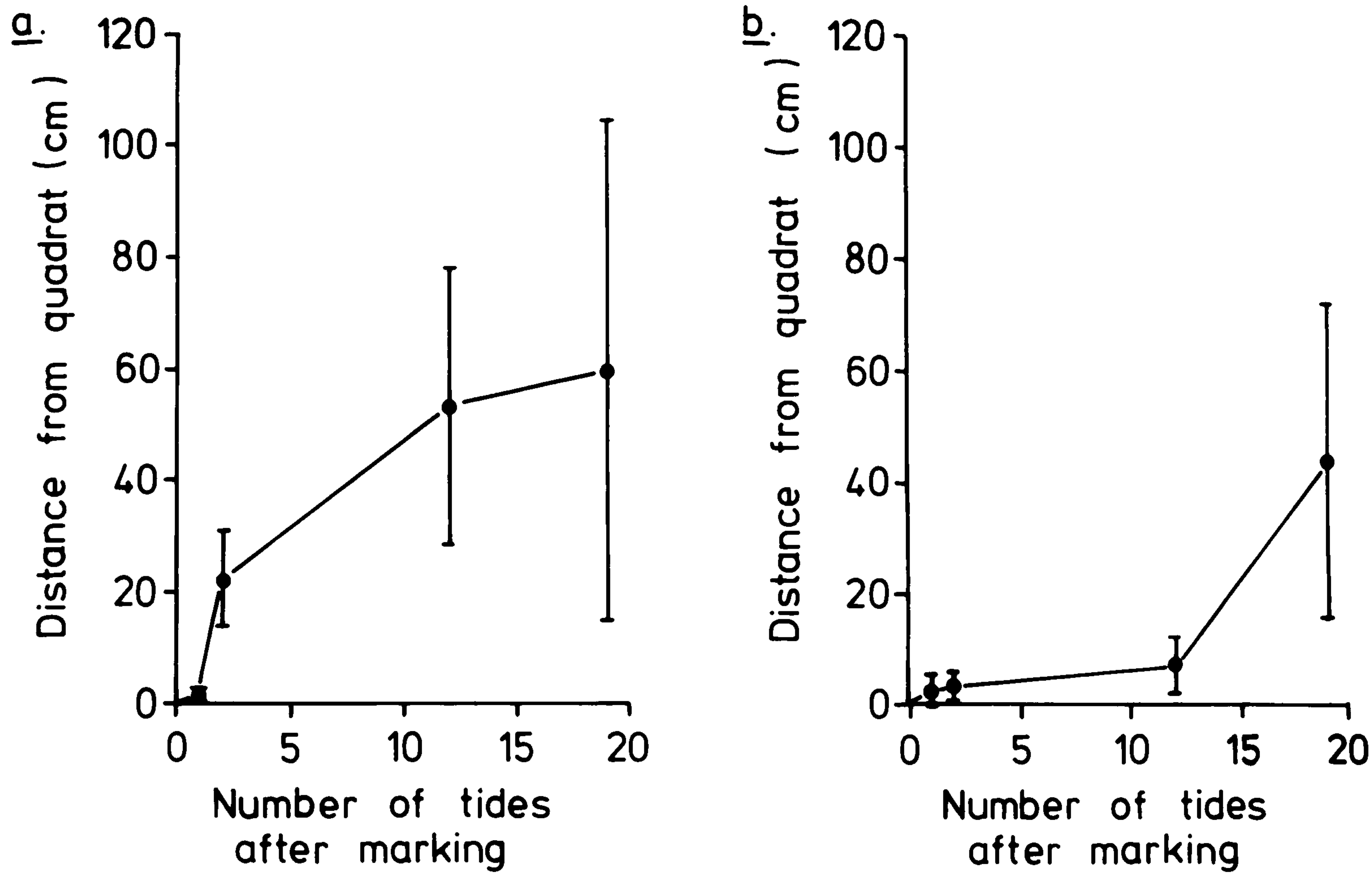


Fig. 54. Mean distance (± 2 S.E.s) moved by Hydrobia ulvae from fhe quadrats on a. Transect BM and b. Transect BS.

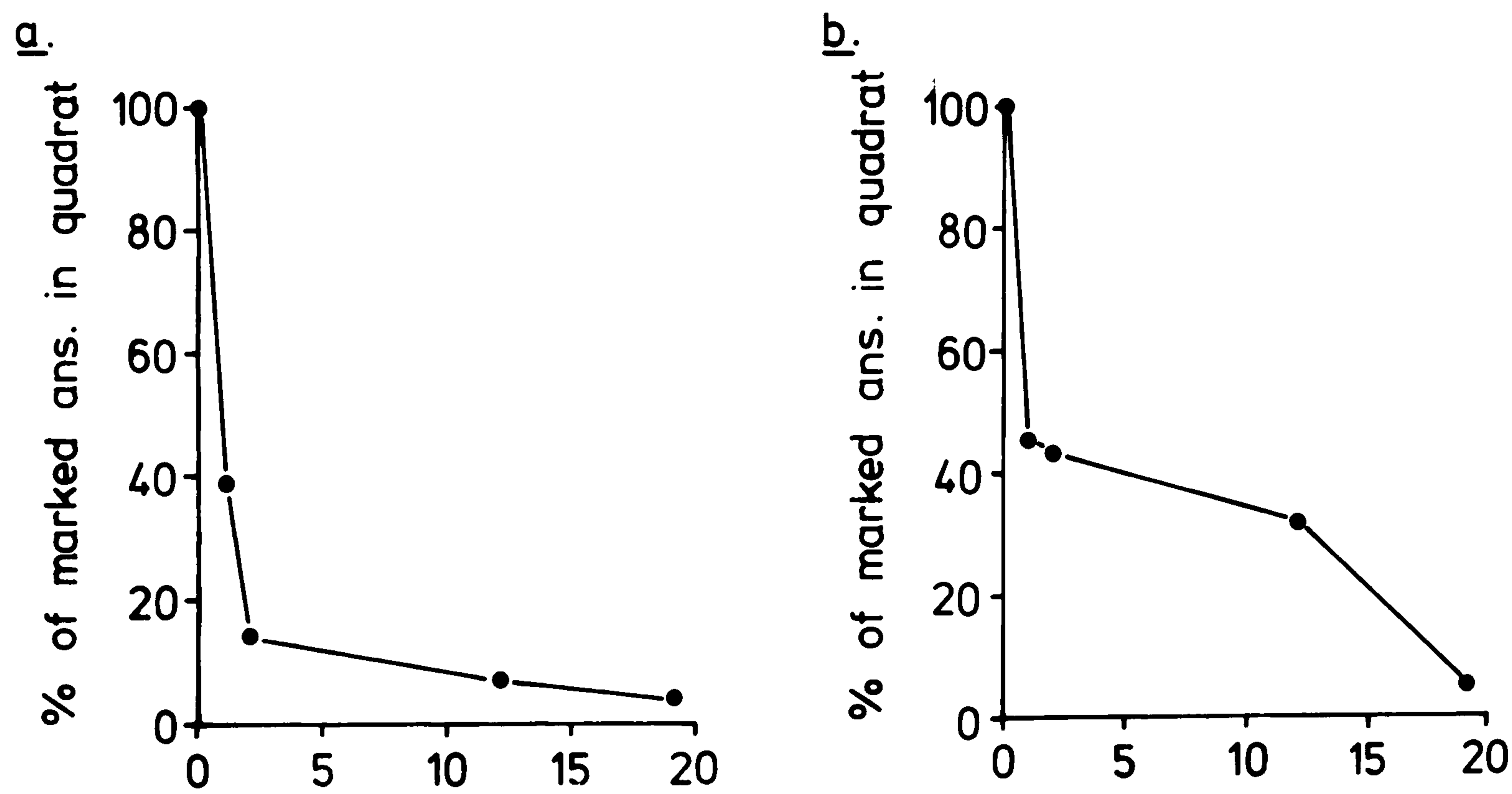


Fig. 55. Percentage of the Hydrobia ulvae originally marked which remained within the quadrats on a. Transect BM and b. Transect BS.

the mean distance moved within Spartina rose to 44 cm, only 15 cm less than that outside. This degree of movement (a mean of approximately ½ m in 19 tides) is quite sufficient to affect the validity of the exclosure results as indicators of predation pressure.

In both transects the percentage remaining within the quadrat dropped by more than 50% during the first high water period. Animals might have been affected by the marking procedure if the paint had trapped air bubbles, since this would have caused them to float away involuntarily with the tide. Alternatively, marked animals may have burrowed beneath the sediment surface before counting took place. The percentage remaining within the transect BM quadrat continued to drop rapidly while the percentage remaining within the transect BS quadrat dropped at a slower rate. After 19 tides both had dropped to approximately 5%.

CHAPTER 7. THE SHOREBIRD FAUNA OF *SPARTINA* MARSHES

i. Shorebird species associated with *Spartina* at Lindisfarne.

Preliminary observations during the winter season of 1971/72 suggested that very few shorebirds occurred within the dense swards of *Spartina*. This was confirmed by incidental observation during the following two seasons. The high density of *Spartina* stems ($238 \pm 23.4/m^2$ at Site B) may account for this by preventing birds from landing easily and also restricting their movement once on the ground. However, birds were found regularly on the open patches of mud between *Spartina* clumps, although they were frequently hidden from view in areas of high clump density. Consequently an attempt was made to minimize the obstructing effect of clumps when selecting areas for quantitative study. Two sites were chosen at Elwick (Site W - Fig. 4) and Budle Bay (Site B - Fig. 2) in areas of contrasting invertebrate faunas. Wooden stakes were used to mark out an area of 100 m alongshore by 200 m downshore at Site W, and 60 m alongshore by 200 m downshore at Site B. Ease of observation and a sufficient number of birds at the two sites were the criteria used in selecting these particular dimensions. In both cases 200 m was sufficiently far downshore to extend just beyond the seaward limit of the main growth of *Spartina*.

Observations at Site B were made from a green canvas hide situated approximately 25 m from the seaward limit of the saltmarsh. At Site W it was not possible to erect a hide and observations were made from the top of a bank 2 m high, approximately 10 m from the landward edge of the *Spartina*.

On a number of days during the 1972/73 season, short observations of a few hours each were made at the two sites. The results were treated as described for the 1973/74 observations (see below) and are given in Appendix V, p 162. This preliminary programme provided a basis from which the main 1973/74 programme was devised.

During the season 1973/74 six days were selected for observation of the use of the Spartina marshes by shorebirds, two at the end of October and beginning of November, two in late January and two in early April. Each pair of days consisted of one with a midday high tide and one with a midday low tide, thus covering the maximum and minimum daylight feeding times available to the birds. Lack of suitable equipment prevented meaningful data from being collected at night. However, incidental observations made under the full moon suggested that night feeding was negligible, possibly because of the mild winter. Data collected and processed according to the day time tidal cycle were therefore considered to be legitimate for comparisons between species.

Severe gales and heavy rain in January produced very atypical bird distributions, driving many inland to the fields. Four Curlew were the only shorebirds observed at Site B during the whole midday low tide observation period for midwinter. Spot checks were made during the following weeks which confirmed that the birds had not returned to the flats, so midday high tide observations for midwinter were abandoned.

On each day, observations were recorded simultaneously at the two sites, by the author at B and by M.W. Pienkowski at W. Observations commenced at dawn and terminated at dusk. Unless disturbance occurred, the numbers of each species which were feeding and the total number of that species present were recorded in each area at 15 minute intervals throughout the day using a 15 - 60 x telescope.

From these results (see Appendix V, p142), both the mean density of each species present in the area and the mean density feeding were calculated for each hour of the low tide cycle. To compare utilisation of the Spartina areas by different species on a seasonal basis, the five days of hourly means were combined to calculate a single seasonal mean for each hour of the low tide cycle.

e.g. Redshank - Site B - 3rd hour after High Water

Observation Days

	31/10/73		8/11/73		30/1/74	
	present	feeding	present	feeding	present	feeding
Observations	3	3	0	0	0	0
	2	2	1	1	0	0
	2	2	2	2	0	0
	2	2	2	2	0	0
Mean	2.25	2.25	1.25	1.25	0	0

	3/4/74		11/4/74	
	present	feeding	present	feeding
Observations	7	7	12	12
	13	12	5	4
	no observation		3	3
	13	12	4	3
Mean	11.0	10.33	6.00	5.50

Seasonal mean for Redshank present $= \dfrac{2.25 + 1.25 + 0 + 11.0 + 6.00}{5}$

$= 4.1$ birds in 1.2 hectares

$= 3.42$ birds/ha

Seasonal mean for Redshank feeding $= \dfrac{2.25 + 1.25 + 0 + 10.33 + 5.50}{5}$

$= 3.87$ birds in 1.2 hectares

$= 3.23$ birds/ha

Results are shown in Figs. 56 and 57. A more simplified comparison was obtained by summing the twelve seasonal means of each species' low tide cycle to give a single total, an 'index of occurrence' (or 'index of feeding').

e.g. Redshank - Site B.

Hours after high water	Seasonal mean density present (Numbers per ha)	Seasonal mean density feeding (Numbers per ha)
1	0	0
2	3.07	2.46
3	3.42	3.23
4	3.38	3.25
5	1.98	1.51
6	2.55	2.34
7	2.00	1.92
8	2.18	1.73
9	2.04	1.92
10	3.33	2.61
11	4.22	3.44
12	1.72	1.57
	Total: 29.89 ('Index of occurrence')	Total: 25.98 ('Index of feeding')

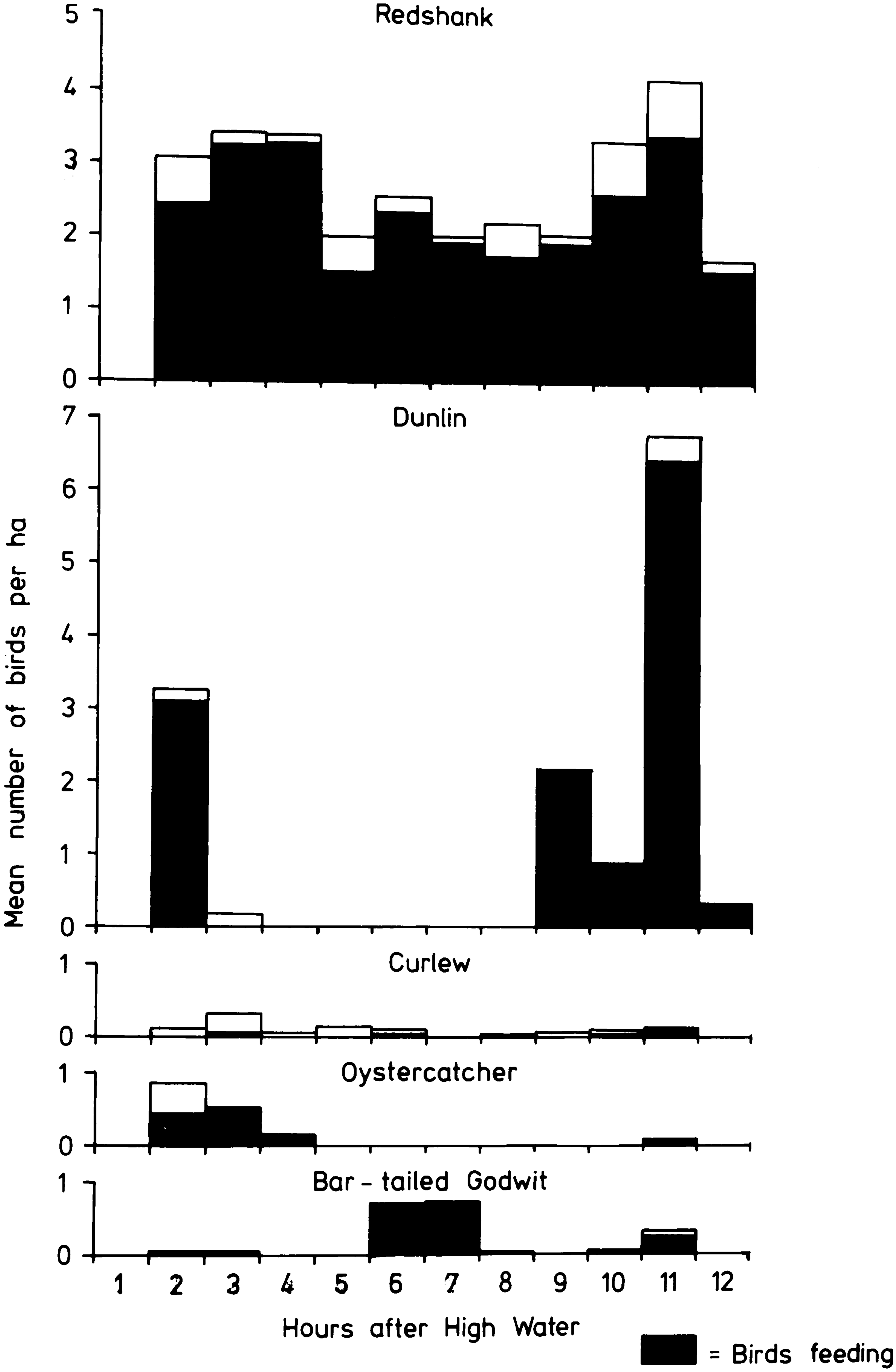


Fig. 56. Seasonal mean densities of shorebirds present and feeding during one low tide cycle at Site B in 1973 / 74.

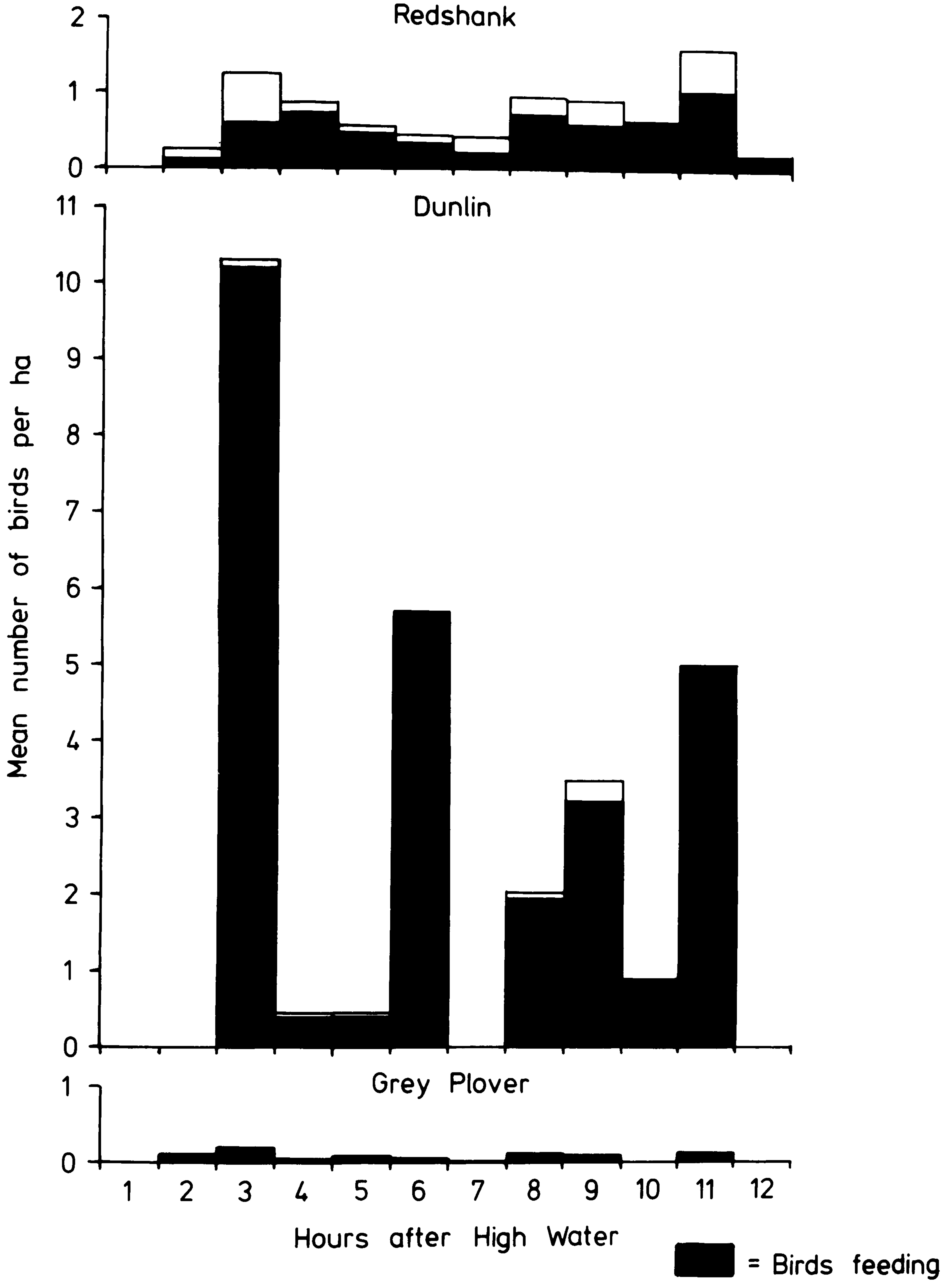


Fig. 57. Seasonal mean densities of shorebirds present and feeding during one low tide cycle at Site W in 1973/74.

These indices are a function of both the mean density of a particular species and the time spent by it in the area. Although of limited absolute value, they are useful quantities for comparing utilisation of the *Spartina* area by two or more species.

Results: -

The shorebird species recorded in the *Spartina* study areas are given in Table 26 together with their respective indices of occurrence and feeding. Those with an index of occurrence of less than one are of negligible importance in the functioning of the *Spartina* community. Of the remaining species, it is quite evident from their indices of occurrence and feeding that the Redshank and the Dunlin are of far greater potential importance in the *Spartina* community than the other species recorded. At Site B the Redshank predominates while at Site W the Dunlin does so. Inspection of Figs. 56 and 57 shows that in addition to the difference in indices of occurrence of the two species, there is a difference in their patterns of appearance through the course of the low tide cycle. In both areas the Redshank is present consistently throughout the low tide period, albeit in smaller numbers at Site W than at Site B. At both sites, however, the Dunlin occurs far more sporadically, usually in large flocks for short periods of time. It is the size of these flocks rather than the time spent in the area that accounts for the predominance of Dunlin over Redshank at Site W, when assessed by an index of occurrence. The majority of the Dunlin population at Lindisfarne feeds on the open mud beyond the *Spartina* and is only forced to feed in the *Spartina* towards the time of high tide.

TABLE 26

Indices of occurrence and feeding for shorebirds at Sites B and W in 1973/74

Species	Site B		Site W	
	Index of occurrence	Index of feeding	Index of occurrence	Index of feeding
Redshank (*Tringa totanus*)	29.89	25.98	7.93	5.50
Dunlin (*Calidris alpina*)	13.57	12.91	28.37	27.85
Curlew (*Numenius arquata*)	1.20	0.33	0.13	-
Bar-tailed Godwit (*Limosa lapponica*)	2.05	1.99	0.15	0.15
Oystercatcher (*Haematopus ostralegus*)	1.70	1.24	-	-
Grey Plover (*Charadrius squatarola*)	0.20	0.20	0.90	0.87
Shelduck (*Tadorna tadorna*)	0.45	0.45	-	-
Turnstone (*Arenaria interpres*)	0.08	0.08	-	-
Mallard (*Anas platyrhynchos*)	0.08	-	0.09	-
Teal (*Anas crecca*)	0.11	0.05	-	-
Knot (*Calidris canutus*)	-	-	1.25	1.25
Lapwing (*Vanellus vanellus*)	-	-	0.05	-

The temporal pattern of these observations suggests that the *Spartina* area may be of more importance to the Redshank than to the Dunlin. The consistent presence of the former among the *Spartina* clumps implies that a definite proportion of the Lindisfarne Redshank population chooses to obtain most or all of its food from this area. An estimate of the size of this proportion is necessary to quantify the importance of the *Spartina* to the Redshank, and is given later. Dunlin, because of their sporadic appearance among the *Spartina*, seem less dependent on this area for their food requirements, although they may have to feed there at times to obtain their daily food requirements (e.g. when lower tidal levels are flooded, especially in cold weather).

Predation pressure on mud-dwelling invertebrates from a bird species feeding in small numbers over a long period of time can be as intense as that from a second species feeding in large flocks for short periods. To distinguish quantitatively between the predation pressures exerted by the Redshank and the Dunlin requires determination of what both birds were taking and at what rate. The nature of the study areas and the small size of the birds, makes this very difficult in the case of the Dunlin, because peck rates cannot be measured and small food items identified by simple observation using a telescope. Consequently a quantitative estimate of predation pressure has been attempted only for the Redshank.

ii. Redshank distribution at Lindisfarne

Quantitative observations were restricted to the 12 square miles of intertidal mudflats and no attempt was made to estimate the numbers of Redshank feeding in the nearby fields. The large area involved made this impracticable, and in addition, occasional observations through the season revealed that the proportion feeding in the fields was negligible, except during the January gales when it increased noticeably.

To determine the preferred intertidal feeding sites of Redshank at Lindisfarne, its distribution was investigated when the available feeding area was at a maximum (i.e. at midday low tide) on three days during the winter season 1973/74. These were in early November, mid-January and late March. The large area involved made it impossible for one person to map the Redshank distribution meaningfully during one low tide cycle. Consequently, the area was divided into a number of sections with one or more observers assigned to each section. All sections were covered simultaneously within about a two hour period around low water, thus minimising the effect of Redshank movements between sections. Any movements that did occur were noted, together with time and direction. The geographical location of each Redshank, or flock of Redshank, was recorded on a sketch map, together with the numbers in each flock and the time of observation. In addition, note was taken of the habitat zone in which the birds were feeding. The zones were classified as follows: -

1. Within the _Spartina_ swards
2. Around the clumps of _Spartina_
3. On open mud
4. Along the tidal or burn edges
5. Other habitats (e.g. sea beaches on the North Coast of Holy Island).

Any birds feeding in the vicinity of very isolated "pioneer" _Spartina_ clumps were assigned to zone 3. Birds flushed from the main swards could either have been feeding amongst the stems of *Spartina*, or on small patches of open mud, and no distinction between these two was attempted during the survey. However, observations of footprints and faeces suggest that most Redshank within the swards confine themselves to the small patches of open mud.

All sketch maps obtained on each day were incorporated into a large map of the whole area. This was divided into ¼ square kilometres and the number of birds occurring in each square was calculated.

a. Overall distribution: -

All 3 maps (Figs. 58, 59 and 60) show a similar pattern of distribution on Fenham Flats. Redshank were concentrated along the High Tidal levels and along the burns and the main channel. They were noticeably fewer or absent altogether from much of the mid-tide zone, in particular where the sediment is coarse. The most noticeable seasonal feature is the restriction of most Redshank to the High Tidal level in January. Strong gales occurred during much of this month and in such conditions in previous winters, Redshank have avoided the exposed parts of the mudflats and have been observed sheltering on the leeward side of *Spartina* clumps. Their ~~virtual~~ almost complete absence from the exposed North coast of Holy Island during January supports this inference. In addition to changes in distribution, the overall population total in January was reduced to approximately 360. Many birds appear to have settled in the more sheltered fields or moved away altogether. As on the Wash (Goss-Custard and Jones - in press) *Crangon* spp. may be an important prey of Redshank feeding in the main channel and on the North shore of Holy Island in Autumn and Spring.

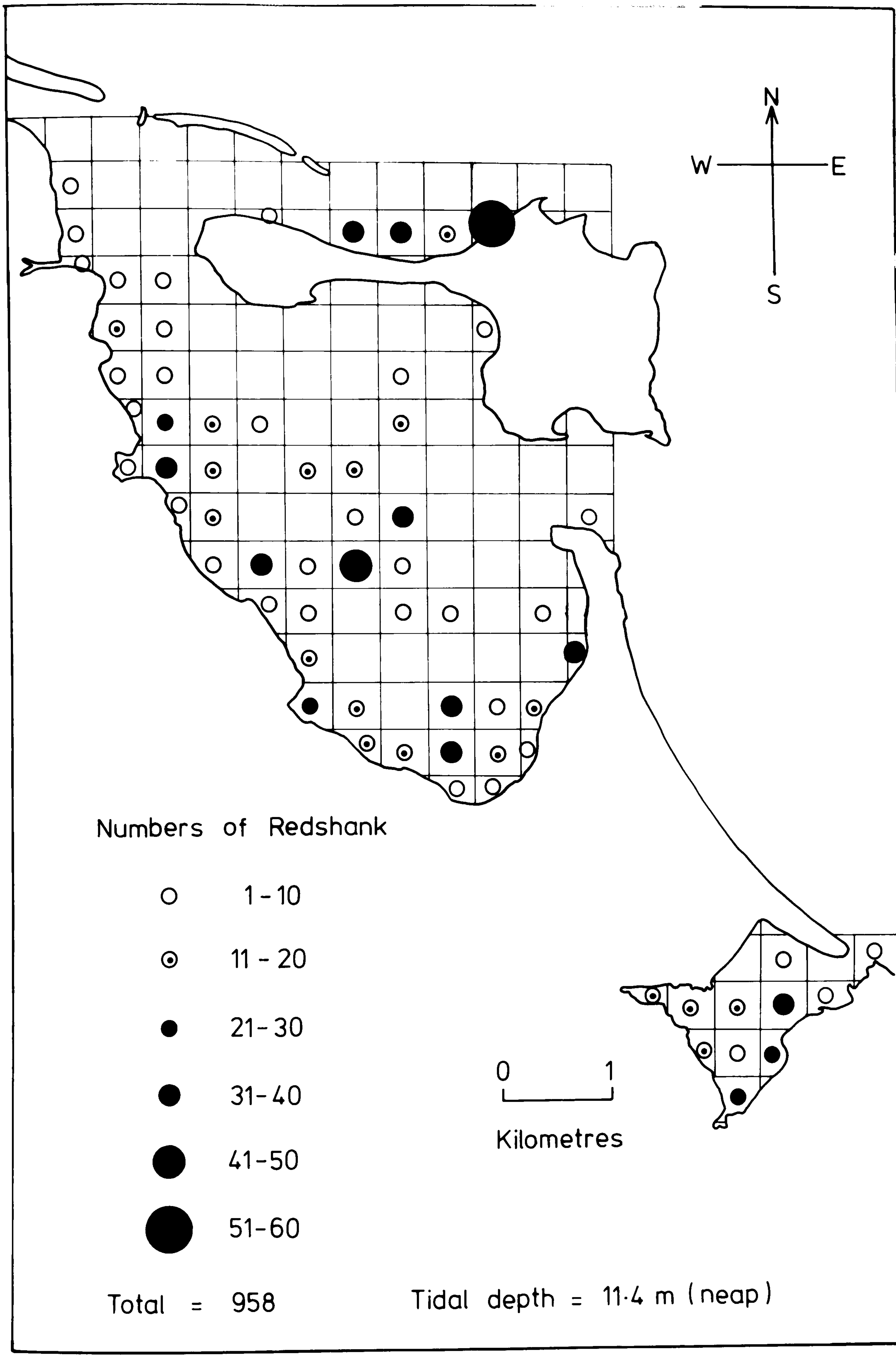


Fig. 58. Low Water distribution of Redshank at Lindisfarne on 1/11/73.

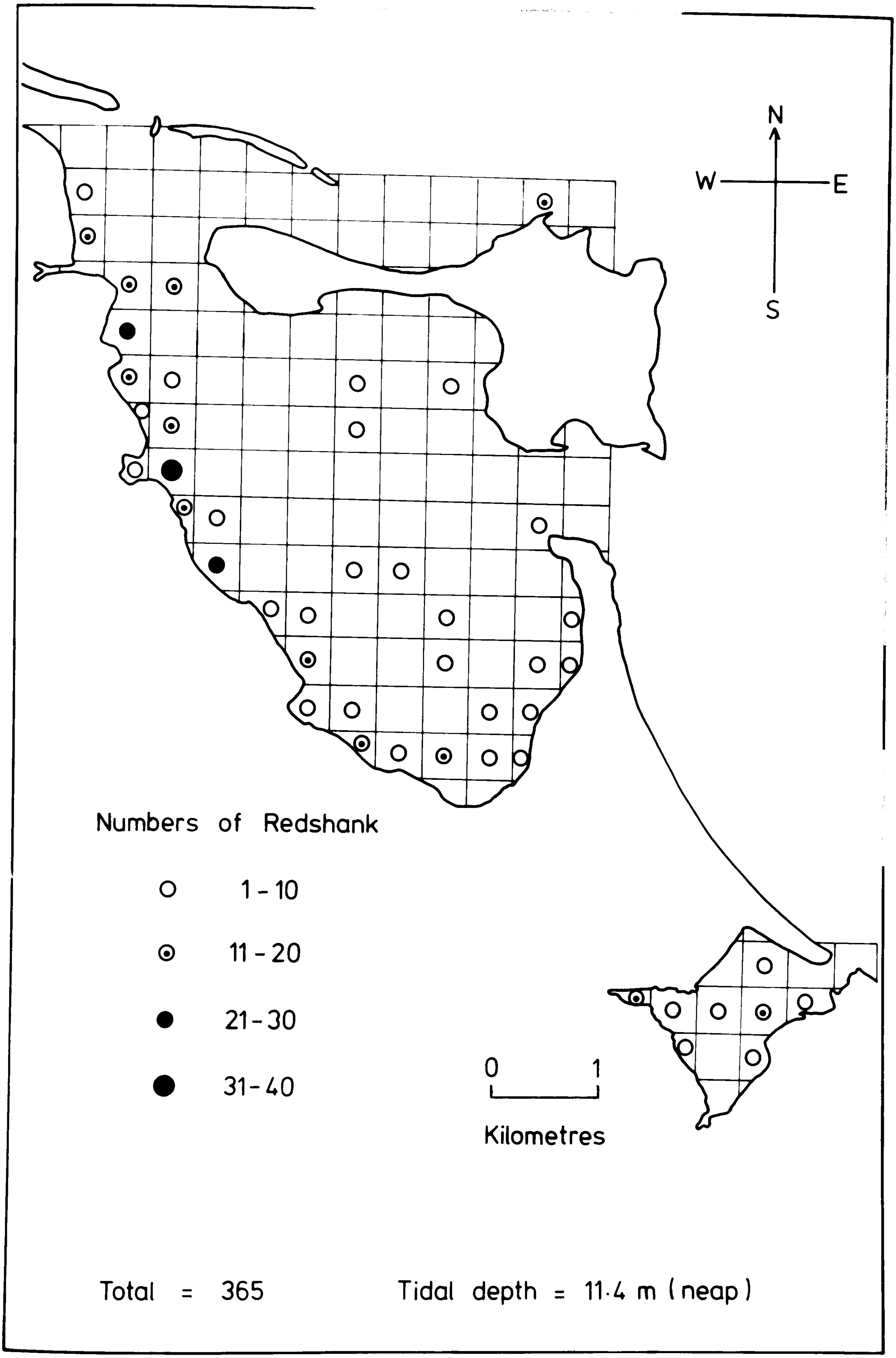


Fig. 59. Low Water distribution of Redshank at Lindisfarne on 17/1/74.

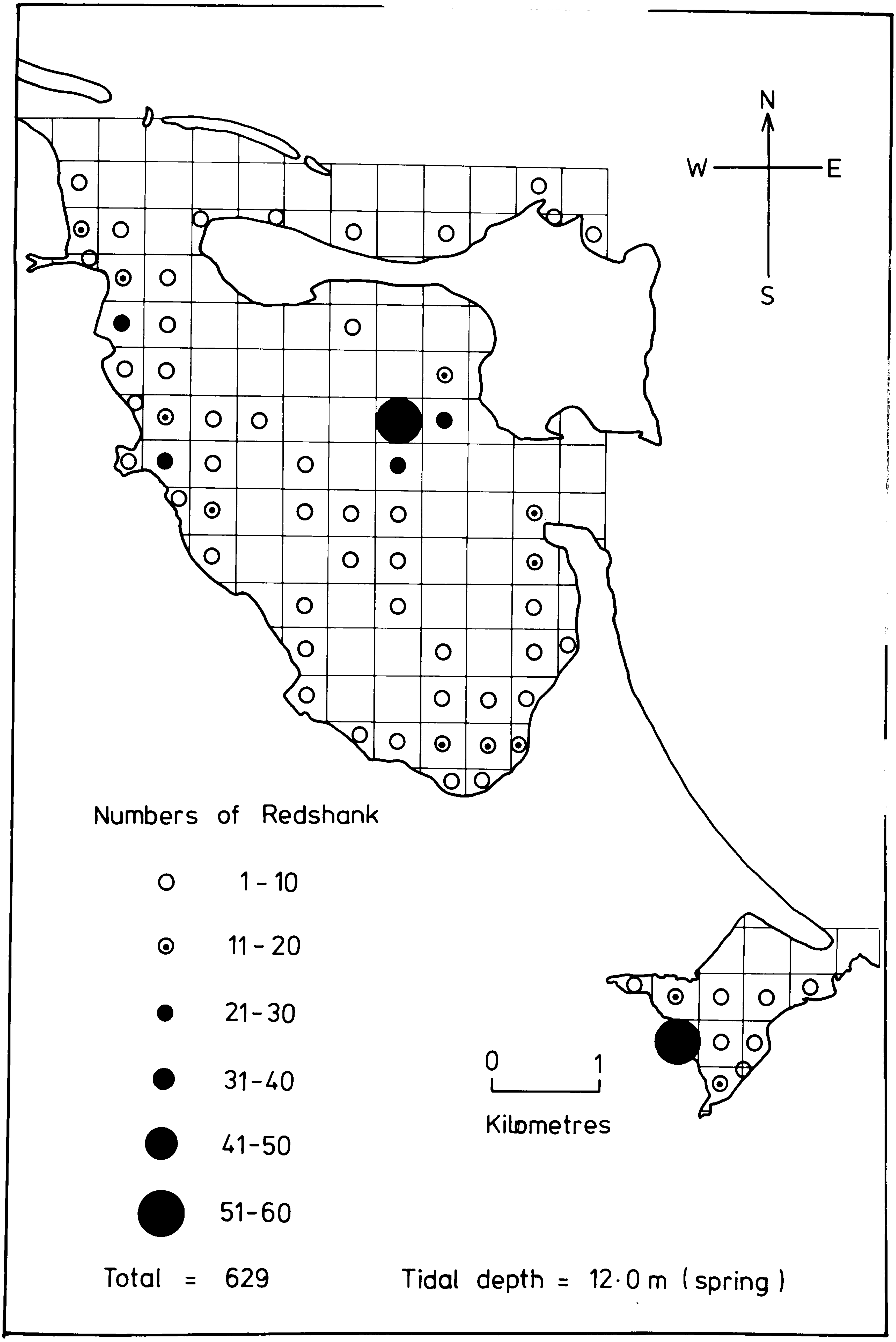


Fig. 60. Low Water distribution of Redshank at Lindisfarne on 28/3/74.

The winter migration of <u>Crangon</u> spp. to deeper waters (Lloyd and Yonge 1947) might therefore be a cause of the movement of Redshank away from these areas in mid-winter. Redshank distribution on Fenham Flats in March was similar to that in early November, (apart from some reduction in the numbers) and presumably represents the chosen distribution of the species when climatic factors are not limiting and preferred prey items are available.

The pattern of distribution in Budle Bay is less clearly defined, partly because of the smaller area involved. Also a higher percentage of the Bay consists of favourable habitat zones and sediments. There is a proportionately greater peripheral High Water zone, and two substantial burns which flow through 10 of the 15 $\frac{1}{4}$ sq. kms. These two factors combined may well account for the wide distribution of Redshank in the Bay. All three maps indicate that the North corner of the Bay was an unfavourable habitat. Ladle (1966) gives a silt percentage of 5 or less for this corner, and the corresponding coarse nature of the substrate is comparable with that on parts of Holy Island Sands in its unattractiveness to Redshank. In January, other parts of the Bay also had reduced Redshank numbers, similar to the situation on Fenham Flats, as would be expected from overall climatic conditions.

b. Preferred habitats: -

On Fenham Flats, (Table 27), the percentage of the Redshank population found within the <u>Spartina</u> sward remained relatively constant throughout the season. However, in the other habitats, the percentage of Redshank fluctuated dramatically. As would be expected, the concentration of Redshank around the periphery of Fenham Flats in January, is reflected in the high percentage associated with Spartina clumps. In late March, reduced numbers in the Spartina clumps were evidently not associated with a return to the open mud. However, 40% of the population were feeding along the burns or in the mid-channel. The spring tide on March 28th (12.0 m) would have exposed more low tide feeding areas than the neap tide on November 1st (11.4 m).

The Spartina swards in ~~Site B~~ Budle Bay contained a low percentage of the Bay's Redshank population in early November and late March. The increased percentage in January is a reflection of the sharp drop in numbers all over the Bay, and not a real increase, since the actual number occurring in the swards was slightly lower than in November and March. The January drop in Redshank numbers at Budle Bay was much larger than the comparable decrease on Fenham Flats, and it would appear that a higher percentage of Redshank from Budle Bay flew inland than from Fenham Flats. This may reflect better feeding in the flooded meadows behind Budle or relatively less shelter among the Spartina in the Bay.

Combined results for the total area indicate that between 28.4% and 62.4% of the Lindisfarne Redshank population feed in association with the Spartina (clumps and swards together) during the daylight low tide cycle, depending on the climatic conditions. This is an appreciable proportion of the population. The majority of these (a mean of 62.7% of those associated with Spartina) feed among the clumps.

A brief investigation of the preferred prey items of the Redshank has been carried out. This, together with knowledge of the

TABLE 27

Habitat preferences of Redshank at Lindisfarne in 1973/74. Results are given as actual numbers (N) and as percentages of the total number observed in the particular area (Fenham Flats, Budle Bay or the two areas combined).

Habitat zone	Fenham Flats						Budle Bay						Fenham Flats and Budle Bay combined					
	1/11/73		17/1/74		28/3/74		1/11/73		17/1/74		28/3/74		1/11/73		17/1/74		28/3/74	
	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%	N	%
Spartina sward	128	16.6	48	14.6	60	12.2	15	8.0	8	22.2	14	10.4	143	14.9	56	15.3	74	11.8
Spartina clumps	95	12.3	169	51.4	105	21.3	34	18.1	3	8.3	54	40.0	129	13.5	172	47.1	159	25.3
i. Open mud	287	37.3	60	18.2	98	19.9	90	47.9	6	16.7	28	20.8	377	39.4	66	18.1	126	20.0
Burn or tidal edge	94	12.2	37	11.3	201	40.7	48	25.6	14	38.9	39	28.9	142	14.8	51	14.0	240	38.2
Other zones (e.g. North shore of Holy Island)	166	21.6	15	4.5	30	5.9	1	0.4	5	13.9	-	-	167	17.4	20	5.5	30	4.7

distribution of these prey items among *Spartina*, and elsewhere, should give some indication of why the Redshank distribution is as it is at the moment, and what the likely outcome is of further *Spartina* sward extension.

iii. The diet of Redshank at Lindisfarne

To compile a list of prey items taken by the Lindisfarne Redshank, when feeding in association with *Spartina*, gizzards of a number of birds collected from the area were examined. The collection of birds for gizzard analysis was difficult since they were very wary and the results obtained can be severely biased by the differing digestion rates of the various prey items. Problems associated with this are discussed fully by Goss-Custard (1973). Since accurate information on the relative amounts of different prey items taken was not required, only a small sample of 17 birds was shot, under licence from the Natural Environment Research Council, during the seasons 1971/72 and 1972/73. The birds were taken from 4 different sites among the *Spartina* (Fenham Mill, Teal Hole, Elwick, Budle Bay - see Fig. 1) at varying times during the two seasons. As far as possible, birds were shot where they had been feeding; where movement had occurred it was usually only from one part of the *Spartina* marsh to another.

Immediately on collection, a 10% formalin solution was syringed into the oesophagus to arrest digestion (Van Koersveld 1951). Within 20 minutes of collection, the oesophagus and gizzard were removed and preserved in 10% formalin. Examination of oesophagus and gizzard contents was carried out under a 10x binocular microscope. The number of each prey species was determined by counting intact individuals and certain characteristic fragments, as discussed by Goss-Custard (1973). He provides a list of suggested fragments for the common prey items of waders, and emphasises the need for different workers to use the same criteria when describing in quantitative terms a bird's diet, so that results can be meaningfully compared. The criteria suggested by Goss-Custard were used in this study and are as follows: -

1. Polychaetes, e.g. *Nereis*: -

   Intact animals; fragments containing the head; individual mandibles (divided by 2).

2. Gastropod molluscs (e.g. *Hydrobia* and *Littorina*): -

   Intact animals; shells where all the whorls are represented.

3. Bivalve molluscs (*Macoma*, *Mytilus* and *Abra*): -

   Intact animals; single complete shells or umbos (divided by 2).

4. Amphipods and Isopods (*Corophium*, *Gammarus* and *Idotea*): -

   Intact animals; fragments with head; 2nd antennae (divided by 2).

5. Decapod crustaceans: -

   Carcinus - Intact animals; complete shells; chelae (divided by 2).

   Mysids - Intact animals; fragments containing head.

6. Insects: -

   Intact animals; fragments containing head.

Methods of presenting the results are discussed by Hartley (1948). In the present study, the frequency is given of each prey species within the sample of seventeen birds, along with the mean number per bird. This was considered the most satisfactory method of determining prey species which are important in the diet of the Redshank, but underestimates the contribution to the diet of soft-bodied animals, e.g. Oligochaetes. Assessment of volume (Hartley 1948, Hynes 1950, Newton 1967) was not thought valid since in many cases there is a major discrepancy between the volume occupied at the time of counting and the actual volume taken in by the bird (e.g. Nereis mandibles).

Results: -

Results for each of the four areas, and the areas combined, are given in Table 28. No attempt has been made to correct for differing digestion rates (Greenwood and Goss-Custard 1970). All major prey items, except Corophium, have been estimated using hard calcareous or chitinous fragments, the digestion rates of which are comparatively slow. In the case of Corophium, the figures as they stand, without correcting for its more rapid digestion rate by comparison with e.g. molluscs, indicate quite clearly that it is a major prey item in three of the four areas.

At Fenham Mill and Budle Bay Corophium, Hydrobia, Littorina, Nereis, Carcinus and Mytilus were important prey species, all of them occurring in at least 50% of the birds at the former site, and at least 67% of the birds at the latter. For both birds collected at Teal Hole Corophium was the most important species, both in frequency (100%) and mean number per gut (70). Elwick is the only area where Corophium was absent from the substrate and consequently did not form any part of the diet. The three main prey species in this area were Hydrobia, Nereis and Littorina, all of which occurred in 75% of the sample.

Taking the four areas combined, it is quite clear that the main prey species for each area fall within a common group of six (Corophium, Hydrobia, Littorina, Nereis, Carcinus and Mytilus), each

TABLE 28

Prey items of Redshank at Lindisfarne. The frequencies (F) and mean numbers per gut (M) are given for each item.

Prey	Fenham Mill 1971/72 (N = 8)		Teal Hole 1972 (N = 2)		Budle Bay 1973 (N = 3)		Elwick 1972/73 (N = 4)		Areas combined (N = 17)	
	F	M	F	M	F	M	F	M	F	M
Corophium	4	1.50	2	70.00	2	8.00	-	-	8	10.35
Hydrobia	4	2.63	-	-	2	9.00	3	2.00	9	3.30
Littorina	4	0.88	-	-	2	3.00	3	12.00	9	3.77
Nereis	6	9.75	1	2.00	2	33.00	3	2.50	12	11.24
Carcinus	4	1.75	1	-	2	1.33	1	0.25	8	1.12
Mytilus	4	4.00	-	-	3	3.33	1	0.50	8	2.59
Macoma	-	-	1	1.00	-	-	-	-	1	-
Abra	3	1.88	1	1.00	-	-	1	0.50	5	0.57
Idotea	1	0.13	-	-	-	-	-	-	1	-
Gammarus	-	-	-	-	1	0.33	-	-	1	-
Coleoptera	3	1.25	1	0.50	-	-	-	-	4	0.71
Mysidacea	-	-	-	-	-	-	1	0.25	1	-
Diptera larvae	1	0.13	-	-	-	-	-	-	1	-

species occurring in at least 47% of the birds collected. Although Nereis would, at first sight, appear to be the most important species, its numbers are based almost entirely on mandible counts alone, and little is known of how long these relatively indigestible fragments remain within the gizzard. A correction factor applied to the Corophium result to allow for its faster rate of digestion, would certainly make it the species with the largest mean number of individuals per bird. However, even without these corrections it is clear which invertebrate species are most important in the diet of Redshank feeding among Spartina.

iv. Invertebrate predation by Redshank at Lindisfarne

The role of the Redshank in the ecology of the mud-dwelling invertebrates can best be quantified by estimating the number of animals taken by Redshanks during one winter season. This figure is a function of 3 components: -

1. The number of Redshank feeding in a unit area
2. The length of time spent feeding (per day x number of days)
3. The rate of ingestion of prey

These 3 components can all vary widely through the season, depending on several factors. For example, component 1. will depend on seasonal movements of the birds, e.g. moving inland during harsh climatic conditions. Component 2. will depend on length of daylight and monthly tidal variations. Component 3. will vary between individual birds and in addition, Goss-Custard (1969) has shown that it is dependent on substrat~~e~~um temperature. To estimate accurately the number of invertebrates removed by Redshank in one winter requires careful consideration of all these variables. However, since individual variation in calorific intake per day is unlikely to be more than 20%, it was considered that relatively few observations would be necessary to ascertain whether Redshank removed most or very few of the invertebrates which disappeared in the wild.

Method: -

Observations on Redshank feeding behaviour were made by the author and M.W. Pienkowski simultaneously at the same 2 sites and on the same days as those used in i.(p 81). No observations were made of night feeding because of the lack of suitable equipment. Most Redshank appeared to stop feeding at dusk and it was hoped that omission of night observations did not introduce any serious errors into the result. The mild winter probably reduced the need for Redshank to feed at night. Predation rates by individual Redshank, feeding within the study areas, were measured during the 15 minute intervals between each shorebird count, by noting the number of successful pecks (swallows) per minute whenever possible. Birds frequently disappeared behind *Spartina* clumps during the course of the minute's observation. In this case, the length of the observation period was noted and all those of less than 15 seconds duration were disregarded. As many minute observation periods as possible were collected for each bird, but obstruction by clumps frequently restricted these to 1 or 2. A mean predation rate was then calculated for each individual bird (see Appendix V, p 163).

Results: -

Individual mean predation rates were combined to investigate a variation with time after high water (Fig. 61) and b variation

Fig. 61. Variation in mean predation rate (± 2 S.E.s) of Redshank with time after High Water at a. Site B and b. Site W in 1973/74.

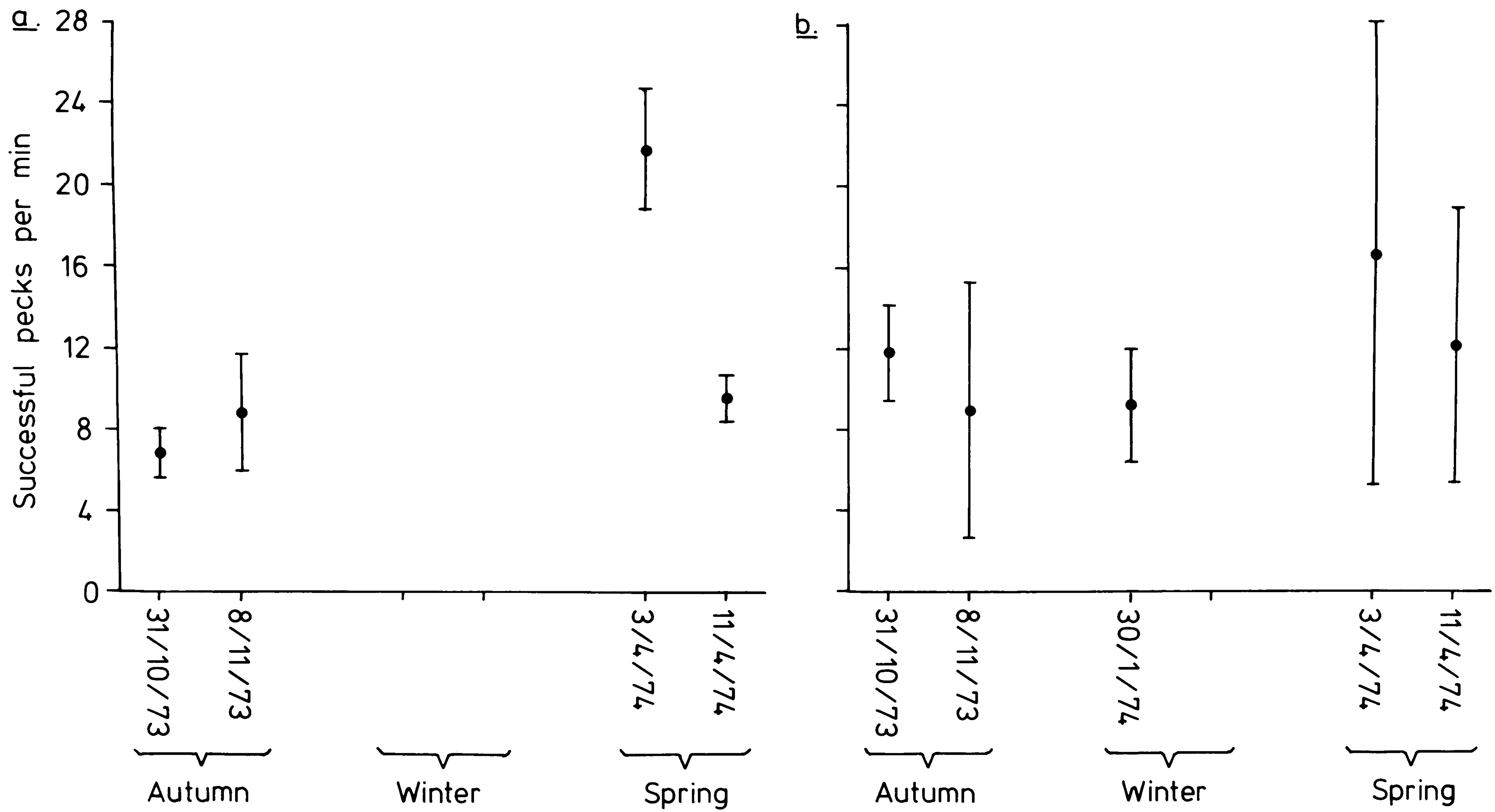


Fig. 62. Seasonal variation in mean predation rate (± 2 S.E.s) of Redshank at a. Site B and b. Site W in 1973/74.

with season (Fig. 62). At Site B there was a non-significant tendency for lower feeding rates around low water, whereas at Site W no clear trends were evident. At both Sites B and W variations in predation rate between seasons were less marked than that between the two spring observation days at Site B. Since predation rate showed no clear trends with either time after high water or season, individual predation rates for 1973/74 were combined to calculate a seasonal mean predation rate for each site. At Site W there were often few Redshank feeding within the area staked out. When this occurred, results were supplemented by observing Redshank just outside the marked area. No difference was found between the mean feeding rate of birds within the area, and that of birds within and without the area combined ($t = 0.124$, $P > 0.1$).

Since intervals between measurement of Redshank feeding behaviour throughout the season were unequal, and mid-winter was represented by one day's observation while Autumn and Spring were each represented by two, separate estimates of the mean density of Redshank feeding at the two sites for Autumn, Spring and Winter were not considered feasible. Instead the seasonal indices of feeding calculated in i. were used as shown below: -

1. Site B.

Seasonal mean predation rate = 12.01 ± 1.56 items/bird/minute

= 720.6 ± 46.8 items/bird/hour

Seasonal mean number of Redshank feeding/ha through 12 hours of low tide cycle (Fig. 56) = 0 + 2.46 + 3.23 + 3.25 + 1.51 + 2.34 + 1. 92 + 1.73 + 1.92 + 2.61 + 3.44 + 1.57 = 25.98 (index of feeding)

∴ Mean daily predation rate per hectare = 720.6 x 25.98

= 18721.2 items removed by Redshank/ha/day.

Length of time exclosure in position = 151 days.

∴ Estimated number of food items removed by Redshank in that time

= 18721.2 x 151

= 2,826,901 items/ha.

2. Site W.

Seasonal mean predation rate = 11.14 ± 3.08 items/bird/minute

= 668.3 ± 184.8 items/bird/hour

∴ Mean daily predation rate per hectare = 668.3 x 5.50 (index of feeding)

= ~~3755.5~~ 3676.2 items removed by Redshank/ha/day

∴ Estimated number of food items removed by Redshank during season

= ~~3755.5~~ 3676.2 x 151

= ~~567,080~~ 555,106 items/ha.

The seasonal mean predation rates for both sites were considerably lower than those found at Aberdeen by Goss-Custard (1969) which were in the region of 60 items per bird per minute at comparable mud temperatures (Lindisfarne mud temperatures never dropped below 6°C on any of the observation days). At Aberdeen above 6°C the diet was predominantly Corophium. At Lindisfarne Corophium was only available at Site B, and at both Sites B and W Nereis was an important prey item. The additional handling time needed to deal with Nereis may partly explain the lower predation rate at Lindisfarne.

During 1973/74, Redshank removed about 5 times as many prey items from Site B as they did from Site W. This was to be expected since there was no significant difference between the mean predation rates by a Redshank in the two areas ($t = 0.504$, $P > 0.1$) and the indices of feeding in the two areas differed by a factor of approximately 4.7.

CHAPTER 8. DISCUSSION

This thesis has been concerned with four main problems. (1) What changes take place in the invertebrate communities of mud flats when colonised by Spartina? (2) Why do these changes occur? (3) Are areas colonised by Spartina still used by shorebirds as feeding sites, and if not, why not? (4) What effects on shorebirds are likely to occur if Spartina spreads further over the mud flats at Lindisfarne? It will be remembered that the problems have had to be studied by simultaneous comparison of areas with and without Spartina, at equivalent tidal levels and similar substrates, since an historical study of changes within a single area would have required longer than the three years available for the project. The answers to the four problems will be considered in turn.

(1) Changes in the invertebrate communities were detailed in Chapter 4 and are summarised in Table 29. As may be seen from Table 30, a general reduction in both the variety of large species and the total number of animals present occurred within Spartina at Site B. The results at Site W and Fenham Mill supported these findings. However, at Site E this trend was reversed with increased numbers of animals and large species occurring within the clumps of Spartina.

TABLE 29

Summary of invertebrate distributions in relation to Spartina at Lindisfarne. A distinction is made between the presence of a species in the summer (S) and the winter (W) at Sites B and E. The larger density of the two is indicated (*) unless there is no obvious difference between them. At Site W and Fenham Mill, where only one sampling programme was undertaken, the presence of a species is indicated by P.

Species are indicated as present if they occurred in one or more samples from the particular habitat (Spartina swards, Spartina clumps and open mud) at a site.

Species	Spartina sward			Spartina clumps		Open mud	
	Site B	Site W	Fenham Mill	Site B	Site E	Site B	Site E
Corophium volutator	S W*	P	P	S W*		S* W	
Hydrobia ulvae	S* W			S* W	S W*	S W	S* W
Macoma balthica				W	S* W	S* W	S* W
Arenicola marina					S* W	S* W	S* W
Nereis diversicolor		P	P	W	W	S* W	
Carcinus maenas	S* W	P		S* W	S W		
Scoloplos armiger	S				S W	S W*	S* W
Littorina saxatilis	S W*		P	S W	S* W	W	

TABLE 30

Numbers of species present (S), mean numbers of individuals of all species present per m^2 (N), indices of diversity (H") and indices of eveness (J) for the invertebrate study areas at Lindisfarne. At Sites B and E summer (Su) and winter (W) results are given separately. Results from *Spartina* swards and clumps are based only on those samples indicated thus ↓ in Figs. 21 to 30 and not on transects as a whole.

	Spartina sward				*Spartina* clumps				Open mud			
	Site B		Site W	Fenham Mill	Site B		Site E		Site B		Site E	
	Su.	W.			Su.	W.	Su.	W.	Su.	W.	Su.	W.
S	5	4	3	3	4	6	6	6	6	7	4	4
N	1001	733	1020	1033	2850	2877	1700	2388	4564	3220	1139	720
H"	0.802	1.149	1.040	1.060	0.541	1.310	1.414	1.073	1.497	1.621	1.059	0.706
J	0.346	0.575	0.657	0.669	0.271	0.507	0.547	0.415	0.580	0.578	0.530	0.353

An additional comparison was made between the communities by calculating an index of diversity (H") for each one from the formula: -

$$H'' = - \sum_{i=1}^{s} \left(\frac{ni}{n}\right) \log_2 \left(\frac{ni}{n}\right)$$

where ni = mean number of individuals of species i per m^2.

n = mean number of individuals of all species per m^2 (Shannon and Weaver 1963)

This measure of diversity depends both on the absolute number of species and on the distribution of individuals between species, i.e. the eveness, which may be calculated as

$$J = \frac{H'' \text{ observed}}{H'' \text{ maximum}}$$

where H" maximum = $\log_2$ S (Tramer 1969).

As might be expected from the number of species present at each site, lower indices of diversity were found within the *Spartina* at Site B and on the open mud at Site E. However, the relatively low values of J within the *Spartina* at Site B in summer, and on the open mud at Site E in winter, indicate that some of the reduction in these indices of diversity was due also to a less even distribution of individuals between species. Although the differences in diversity between the *Spartina* and open mud at Sites B and E were small they were consistent over both summer and winter. It must be remembered that no attempt was made to examine any small species present, so that the meiofaunal component of the community has not been included in the above comparisons.

(2) It is quite clear that colonisation of mud flats by *Spartina* does lead to a change in the invertebrate community, although the nature of

this change can vary significantly. However, it is less easy to isolate the factors which bring about this change, and to attempt to do so requires consideration of how *Spartina* might affect the sediment in which the invertebrates exist.

Although differences between sediment characteristics inside and outside areas of *Spartina* (Chapter 3.) could have led to the present *Spartina* distribution, the widely known ability of *Spartina* to accrete silt rapidly (Ranwell 1964a) suggests that the high silt/clay content within *Spartina* at Site B is almost certainly an effect of *Spartina* growth. At Site E the much lower silt/clay content within *Spartina* may have resulted from the more exposed position of the site and the lower density of the *Spartina* (Chapter 2, p 15). Both these factors would tend to prevent sufficient slowing down of water currents to allow the settlement of fine particles.

Many of the differences in sediment properties within and outside *Spartina* are associated with the high silt/clay content within the sward. The close relationship found between particle size and *i* carbon content and *ii* nitrogen content at both sites support the findings of Newell (1965). The high silt/clay content within *Spartina* includes appreciable amounts of organic detritus. Odum and De La Cruz (1967) found a much greater weight of ash-free dry organic matter per litre (2 - 20mg) at the mouth of a small tidal creek draining a *Spartina* saltmarsh at Sapelo Island, Georgia, U.S.A., than had been found for open seawater and other fertile locations (e.g. Plymouth Bay and Long Island Sound) where particulate organic matter was approximately 1 - 3 mg per l. This high organic proportion of the silt/clay fraction from *Spartina* marshes is clearly reflected in the high carbon content of the sediment. The large surface area per unit volume of smaller particles allows a high population of micro-organisms to exist, using the dead organic detritus as a substrate for their nutritional requirements. Thus the nitrogen content, which reflects to a large extent the density of micro-organisms (Newell 1965, Meyer 1973), is closely related to the particle size of the sediment.

At Site B the negative correlation between particle size and depth of the Redox-Potential-Discontinuity (R.P.D.) supports the conclusions of Fenchel and Riedl (1970). Below the R.P.D. the accumulation rate of organic material available to micro-organisms is greater than the rate of oxygen input sufficient to oxidise this material and hence anaerobic reducing conditions develop. Thus, within Spartina marsh, the high silt/clay content, which decreases circulation of interstitial water and thus oxygen, and also reflects a high organic content, raises the R.P.D. nearer the sediment surface.

The high interstitial water content of sediment within Spartina at Site B is also associated to some extent with the high silt/clay content. The capillary force exerted by small particles of sediment allows greater retention of water against evaporation and slower drainage through the sediment, than larger particles (Webb 1958). The presence of Spartina also affords some shelter from strong air currents and hence reduces evaporation of the surface layer of water. Other factors such as permeability of the underlying rock and freshwater seepage from above MHWS may also affect the interstitial water content of the sediment, but are not universal features of Spartina marshes.

Thus the differences found between sediment properties inside and outside Spartina, particularly at Site B, can be explained largely by the spread of the Spartina itself, and by consequent rapid accretion of large quantities of silt. The similarity in particle size inside and outside Spartina at Site E probably accounts for the lack of other consistent differences between sediment characteristics.

At both sites the negligible variation in salinity between Spartina and open mud is most unlikely to account for any variations in invertebrate abundance. In addition, the minimum salinity encountered (12.08‰), which was considerably lower than the rest, was above the known minimum tolerance of all the invertebrates encountered (Table 31).

In view of the largepotential food source available to deposit- and suspension-feeders within the Spartina, it is surprising perhaps that few species appear to thrive within the swards and some are absent altogether. For species other than Corophium and Hydrobia, studies were made only on distribution and densities. These findings will be discussed and interpreted in the light of previous workers' findings. Discussion of my more detailed studies on Corophium and Hydrobia is presented later.

i. Arenicola.

Of those invertebrate species encountered in the study, two (Arenicola and Macoma) were completely absent from within the extensive Spartina swards. Although Arenicola is considerably resistant to anaerobic conditions (Hecht 1932), it is absent from very fine particled mud which would otherwise clog its respiratory surfaces (Eltringham 1971). In addition, the high silt/clay content with accompanying high interstitial water content, which together produce a

TABLE 31

Known minimum salinity tolerance of invertebrates encountered at Lindisfarne

Species	Minimum salinity tolerance		Reference
Corophium	2°/oo	For occurrence	McLusky 1967, 1968
"	7.5°/oo	For breeding	McLusky 1967, 1968
Hydrobia	10°/oo		Muus 1963
"	1.7°/oo	Possible different physiological races varying in tolerance	McMillan 1948
Macoma	6.8°/oo	Survives indefinitely in laboratory	Dunn 1967
Arenicola	8°/oo		Schlieper 1929
Nereis	1°/oo		Smith 1955a
Littorina	8°/oo		Green 1968
Carcinus	6°/oo		Webb 1940
Scoloplos	7.7°/oo	Adults in the Baltic Sea	Mulicki 1957
"	14.4°/oo	Larvae in laboratory	Gibbs 1968

soft, fluid sediment within the *Spartina* sward at Site B, would make burrowing very difficult, since Newell (1972) states that if the sediment remains in a semi-fluid state for long, *Arenicola* is unable to grip the walls of a burrow to penetrate deeper into the mud. The total absence of *Arenicola* from within the *Spartina* clumps at Site B may also reflect difficulties in burrowing and respiration since, although the silt/clay contents are lower than within the extensive swards, they are still considerably higher than the corresponding values within *Spartina* clumps at Site E where *Arenicola* does occur. At both Sites B and E predation of *Arenicola* by shorebirds such as the Curlew (P.C. Smith pers. comm.) and Bar-tailed Godwit (Smith 1975) accounts only in small part for the smaller winter densities, since both birds feed chiefly at lower tidal levels. Spawning of *Arenicola* in Great Britain has been reported in the autumn (Duncan 1960) and in the spring (Howie 1959) and is usually followed by a 40% mortality among adults (Newell 1948). Without detailed information on spawning at Lindisfarne, it is obviously very difficult to interpret properly seasonal changes in distribution and abundance, the more so since young *Arenicola* may move to lower tidal levels during their first year of life.

ii. *Macoma*.

Macoma, the other species absent from within *Spartina* swards, burrows normally to a depth of between 5 and 10 cm. The extensive root network of *Spartina* may adversely affect its ability to burrow, although its presence within the *Spartina* clumps at Site B in the winter and Site E in both the summer and the winter suggest that this effect is not very great. Newell (1965) discovered an increased density of Macoma in sediments with a higher silt/clay content. However, both Fraser (1932) and Dunn (1967) found that above a certain maximum silt/clay level, Macoma was absent altogether. Although they both defined silt differently from this study (Fraser: - as that fraction less than 50μ in diameter; Dunn: - as that fraction less than 63μ in diameter), the maximum silt/clay levels found for Macoma (between 60% and 80% by Dunn and 70% by Fraser) were comparable with the values of between 76% and 98.5% which I obtained for a slightly coarser silt (mean diameter 126 ± 8.2μ) within the Spartina sward on transect BS. Van Benthem Jutting (1959) suggested that the strong reducing conditions associated with high silt/clay contents are detrimental to Macoma although Dunn found high densities of Macoma (up to 1645 per m^2) in an area where the R.P.D. was only 1 cm below the surface. Fraser suggested that a high silt content in the water might block the breathing apparatus but there is no experimental evidence to support this. However, Loosanoff and Tommers (cited by Jørgensen 1966) found that increased concentrations of silt depressed the filtration rate of the suspension feeding bivalve Crassostrea viginica. Since Macoma can behave as a suspension feeder (Brafield and Newell 1961), Dunn suggests that high silt contents of both sediment and overlying water would have a similar depressive effect on the filtration rate of Macoma. This may indeed be the case within the extensive Spartina swards although it is also possible that the extremely shallow R.P.D. (3 mm below the surface within the Spartina sward at Site B) may reflect considerably more unfavourable conditions for Macoma than at the site where Dunn found a density of 1645 per m^2. The high interstitial water content and consequent fluid sediment within the *Spartina* sward on transect BS may also prevent *Macoma* both from burrowing easily and moving horizontally across the sediment surface (as described by Brafield and Newell 1961) by reducing the grip offered by the sediment to the foot. In those places where *Macoma* did occur at Lindisfarne, the tendency for summer densities to be higher than winter ones at both Sites B and E may reflect a considerable loss in the autumn, possibly through predation, or by emigration to lower tidal levels.

iii. *Nereis*

Although *Nereis* was absent from the extensive *Spartina* sward at Site B, its presence in swards at both Sites W (up to 1200 per m^2) and Fenham Mill (up to 1300 per m^2) indicates that it can survive well in *Spartina*. The higher densities of *Nereis* towards MHWS, together with its distribution limits of 150 m downshore from MHWS at Site B and 60 m downshore at Site E and Fenham Mill, are characteristic of its upper shore distribution as noted by Stephen (1930) and Brady (1943). Its ability to survive in conditions of varying salinity (Smith 1955a, 1955b, 1956) probably accounts for its existence in upper shore zones where freshwater runoff is likely. Unlike *Arenicola*, *Nereis* is unlikely to be affected adversely by the high silt content within the *Spartina* swards. Its catholic feeding habits indicate that it is a far more active animal than *Arenicola*. [Perkins (1958) examined the gut contents and detected diatoms, turbellarians, nematodes, polychaete chaetae, copepods, ostracods, appendages of other arthropods, copepod eggs, vegetable matter and detritus]. This suggests that it emerges freely from the sediment during high water and hence respiration would not be affected adversely by a high silt/clay content. At low water the head of Nereis emerges from the burrow and passes undulatory waves down the body which draw in a series of air bubbles which are then trapped between the body and the tube. When they have reached the posterior end of the body, movements cease and the bubbles are held against the body for a few minutes before a further set of irrigation movements is set up (Newell 1972). Hence Nereis can exist in anaerobic sediments during the low tide period.

iv. Scoloplos.

Since Scoloplos usually avoids the black reduced layer (Vader 1964), it is surprising that it was found within the extensive Spartina sward at Station BS 90 where the depth of the R.P.D. was only 3 mm. Brady (1943) also noted the absence of Scoloplos from "highly organic soils". Scoloplos feeds in a similar way to Arenicola, by extrusion and retraction of the proboscis (Newell 1972). However, it has no permanent burrow (Vader 1964), but moves continually through the oxidised layer of sediment and is never found on the surface. It has a wide intertidal distribution (Brady 1943, Ladle 1966), tending to prefer sand containing appreciable quantities of organic debris (Stephen 1930). Brafield (1964) noted that it was abundant only between mean percentage saturation values of 3 to 8.5% oxygen, although this may reflect optimum food conditions rather than its tolerance for oxygen. From these previous observations it is clear that the sediment found within extensive Spartina swards is probably unsuitable, being largely anaerobic with a very shallow, fluid, oxidised layer in which the animal could burrow. Highest densities of Scoloplos at both Sites B and E were found in open mud where the absence of the

Spartina root system may allow much easier burrowing.

v. *Carcinus*.

The total absence of *Carcinus* from open mud almost certainly reflects the lack of shelter available. *Carcinus* colonises a wide range of habitats from rocky shores to mudflats and saltmarsh pools, but is clearly most abundant where shelter is available (Green 1968). Within the swards and clumps of *Spartina* by day, *Carcinus* is sheltered from predatory birds (e.g. gulls) and can easily burrow beneath the surface of the fine, soft, fluid sediment. Naylor (1958, 1960) discovered rhythmic patterns of locomotory activity in *Carcinus*, with peaks coinciding with high water and darkness. It seems possible, therefore, that *Carcinus* may emerge from the *Spartina* during the night or high water period and forage for food on the open mud or under water. It is a generalised predator, eating most things that it catches or finds (Green 1968). During the low tide period, respiration in the black, largely anaerobic sediment found within *Spartina*, can be achieved by *Carcinus* raising the openings between its antennae above the sediment surface and taking bubbles of air into the gill chamber. These are passed through the water bathing the gills by the action of the scaphognathite (Arudpragasam & Naylor 1964a, 1964b).

vi. *Littorina ('saxatilis')*

Higher densities of *Littorina* within *Spartina* at both Sites B and E may also partly reflect the shelter offered by the *Spartina*. Green (1968) states that *Littorina* feeds on detritus, diatoms and other small algae which are scraped from the surfaces over which it moves. Although diatom densities were low within *Spartina*, there were high densities of bacteria (Meyer 1973) and large amounts of detritus for the animals to feed upon. Also, *Spartina* clumps provide a stable anchorage system around which filamentous algae grow in large quantities. At Site B higher densities of *Littorina* within the clumps than within the sward could have arisen because of several factors. Although *Littorina* can use aerial respiration (Sandison 1966, 1967) and thus easily survive within the *Spartina* swards during low tide, the food available may be more attractive within the clumps where more green alga was present. Also, browsing excursions by *Littorina* may be more frequently stimulated among the more wave-exposed clumps than within the sheltered extensive swards. [Newell (1958) found that the closely related *Littorina littorea* requires the stimulation of increased wave action, such as occurs during flowing or ebbing of the tide, to initiate browsing].

vii. *Corophium*.

At Site B, both in summer and winter, the distribution of *Corophium* suggests a reluctance or inability to colonise *Spartina*, particularly the extensive swards. This was supported by findings at Site W where the species was restricted to the landward end of the sward. Although it was present within the sward at Fenham Mill, densities were very low (less than 500 per m^2). However, at Site B during winter, the density within the *Spartina* increased noticeably while that on the open mud decreased and the species was absent more than 150 m downshore of MHWS. These points require consideration, as do the larger mean size and weight of *Corophium* within *Spartina* during December and the larger mean size during May.

Before discussing the factors which might have brought about the particular distribution of *Corophium* at Lindisfarne, it is necessary to consider to what extent the June and December estimates of Corophium distribution and abundance were representative of the true situation. Clearly, over a period of months, movement is an important element of the distribution of mobile species such as Corophium. Migrations of Corophium populations have been recorded by Quatrefage (cited by Bates and Westwood 1863) who stated that animals migrate upshore at the end of April and return suddenly at the end of October, and by Watkins (1941) who found that during the course of a year, a population on the River Dovey also shifted, probably because of mud drying out in the summer. In addition to movements of whole populations, movements of individuals within populations have also been observed. Meadows and Reid (1966) noted that larger animals do not remain permanently within their burrows but emerge after one or more days and explore the surface of the mud, periodically moving to new burrows. Morgan (1965) found that Corophium in the laboratory responded to reduced hydrostatic pressure by swimming, and observed in the field that they left their burrows on the incoming tide, crawled on the mud surface and then tended to swim more as the tide ebbed. Similar observations were made at Site B when Corophium were seen to be swept along by the tidal current for up to a metre while swimming. Under such circumstances it seems unlikely that they would return to their original burrows. These observations all suggest that the movements demonstrated in the dye experiments were not induced by the experiment itself. The degree and form of movement indicated a small-scale multi-directional movement of individuals within a population. It is unlikely that such movement permits a regular large-scale interchange of animals over the 140 m separating transects BM and BS. Also, no major changes in sediment occurred at Lindisfarne which might have induced a whole population to move (as observed by Watkins). I conclude that although small-scale movements within separate areas, such as the Spartina sward or the open mud, will take place (together with a little movement across the border between Spartina and the open mud), the June and December distributions of Corophium adequately represent relatively permanent seasonal distributions, rather than a dynamic balance involving continual large-scale movement of a majority of animals between the Spartina and the open mud. If such movements had occurred, no differences would have been expected in lengths or weights of animals in the two habitats, yet such were found.

Before discussing further the spatial and temporal differences in Corophium densities, comparisons to be made are summarised in Table 32, together with indications of their reliability.

Although Meadows (1964a) demonstrated that Corophium preferred fine sediments, my study of habitat selection at Lindisfarne clearly indicated that, at above 50% silt, Corophium was either present in very low densities or absent altogether. The fact that five out of six stations with silt/clay contents higher than 50% occurred within Spartina suggests how Spartina might affect Corophium, i.e. through sediment factors associated with it. The tendency, albeit non-significant, for Corophium to remain swimming longer above Spartina sediments than open mud further suggests that the sediment within Spartina swards may be unattractive to Corophium for reasons other than particle size. Meadows (1967) showed that previous experience in atypical substrate did not alter the preference of Corophium for typical substrate. It seems unlikely therefore that Corophium swam longer over Spartina sediment because they had existed previously in a different substrate.

TABLE 32

Summary of possible comparisons between *Corophium* densities

	Within Spartina		*Open Mud*	
	WINTER	⟵ Comparison reliable ⟶	WINTER	
Comparison much less reliable, large-scale movements more likely	↕		↕	Comparison much less reliable, large-scale movements more likely
	SUMMER	⟵ Comparison reliable ⟶	SUMMER	

(Small-scale movements which are unlikely to affect comparison)

N.B. This table of possible comparisons applies also to the discussion of *Hydrobia* results presented later.

More probably, any preference that existed for open mud was a genuine avoidance of the sediment found within Spartina.

The absence of Corophium from sediment within Spartina may be associated with the very shallow R.P.D. (3 mm below the surface for all three stations within the Spartina sward on transect BS). Delage (1881) stated that Corophium was not found "if decaying organic detritus renders the mud black", and both Hart (1930) and Gee (1961) noted the absence of Corophium from black, sulphide-smelling mud. Although Corophium has been shown to prefer anaerobic mud to aerobic mud (Meadows 1964a, b), it seems likely that the highly reducing conditions 3 mm below the surface of the Spartina sediment, with the attendant high concentrations of sulphides and hydrogen sulphide (up to 700 mg per l in the interstitial water of sediment - Fenchel and Riedl 1970) may deter Corophium from burrowing. The high interstitial water content within the Spartina sward may also act as a deterrent by preventing construction of stable burrows in the fine silt. Gee (1961) claimed that Corophium inhabits the areas where the water content is not much above 40%; whereas within Spartina swards, the water content was approximately 70%.

The increased density of Corophium at the landward end of transect BC in winter is difficult to interpret since no winter sediment parameters were measured. A lowering of the R.P.D. during winter (Perkins 1957) may account for the presence of Corophium within the Spartina sward (BS 30) and the greatly increased density at BC 90, although there was no direct evidence that the R.P.D. was lower. The dramatic decrease in transect BM could reflect greater predation on the open mud, or greater exposure to winter climatic conditions.

The establishment of an exclosure on transect BM during the winter of 1973/74 produced a major difference between densities inside and outside the exclosure by spring. It seems unlikely that this was due entirely to predation by Redshank, for reasons stated earlier (see Chapter 5, v, p 58). Even assuming an equal degree of predation by Dunlin, and the likelihood of some predation by fish species (such as the Flounder), it is unlikely that this would account for the discrepancy between the exclosure estimates and direct observation estimates of *Corophium* removal by Redshank. More probably, this discrepancy was due to movement of *Corophium* into the exclosure because of the higher silt/clay content found there. Although my own examination of *Corophium* density in relation to silt/clay content was inconclusive, the work of Meadows (1964a) indicated clearly that, within the range of particle size encountered in and around the exclosure, *Corophium* preferred finer sediments.

Despite the somewhat irrelevant exclosure results, direct observations indicated that just under 300 items of *Corophium* size were removed from each square metre of open mud at Site B during the winter season. Analysis of gut contents of Redshank at Budle Bay showed that *Corophium* was indeed taken, but since other small species were found (e.g. *Hydrobia*, *Littorina*) which could not be distinguished from *Corophium* by field observation, less than 300 *Corophium* per m^2 were removed by Redshank during the season. Clearly predation alone, by Redshank and the other less important shorebird predators, will not explain the winter drop in *Corophium* density from approximately 2000 per m^2 to less than 500 per m^2 for much of transect BM. It is possible that climatic factors (e.g. the washing away of sediment during autumn gales) may have had greater impact on the more exposed population of *Corophium* in the open mud.

The larger *Corophium* found inside the *Spartina* could either indicate lower mortality within the *Spartina* or a net movement of older size classes into the *Spartina*. Although older size classes move more than younger ones (Meadows and Reid 1966), it seems unlikely that wholesale migration of larger animals would take place to an area where much of the sediment may be unfavourable to *Corophium* because of the shallow depth of the R.P.D. Since Redshank prefer *Corophium* above 4 mm in length (Goss-Custard 1969) and negligible predation by shore-birds was observed within the *Spartina*, it seems likely that removal of larger *Corophium* on open mud may have reduced the mean size of animals there to below that found within the *Spartina*. In addition, the greater size of *Corophium* within the exclosure was due mainly to a larger percentage of the 6 - 7 mm size class. The difference between size of *Corophium* inside and outside the exclosure is not great enough to be explained by differential movement as described by Meadows and Reid (1966). Moreover, no evidence of greater movement amongst the larger size classes was found in the experiments at Site B.

The difference between dry weights of *Corophium* inside and outside *Spartina* in December is not easy to interpret. It is surprising that the difference was not maintained until the summer, at least among the larger animals where it is conceivable that differentials would have been greater. This implies that during spring either *Corophium* outside *Spartina* put on weight faster than those inside, or there was selective death of lighter individuals outside *Spartina*. Alternatively, the difference detected in winter was not a true one. In this context, it should be remembered that fewer animals were available from within *Spartina* than from outside and hence mean values were based on different sample sizes. Moreover, these differing sample sizes may have biased the result from a whole area in favour of one station from that area. Hence, there may be undetected variations within areas which make true comparisons between areas difficult. Assuming the winter difference to be true, either food supplies outside *Spartina* were at a level sufficient for normal *Corophium* growth and maintenance, whereas food supplies inside *Spartina* were in excess (thus resulting in energy storage), or those inside were sufficient for normal growth and maintenance of *Corophium* and those outside were deficient for optimum growth of *Corophium*. Since by far the largest densities, even in winter, were found outside *Spartina*, the latter seem very unlikely. Little is known about energy storage in amphipods and further work is clearly needed to determine whether the weight differences were true ones and if so, what accounted for them.

viii. *Hydrobia*.

At Site B the distribution of *Hydrobia* indicates a greater tolerance of *Spartina* than that shown by *Corophium*, although *Hydrobia* was found in appreciable numbers only beyond 60 m downshore from MHWS in both summer and winter. At both Sites W and Fenham Mill, *Hydrobia* was absent from the sward, which in both cases did not extend downshore beyond 60 m from MHWS. In contrast, at Site E, *Hydrobia* distributions in both summer and winter indicated a strong preference for the *Spartina* area. As with *Corophium*, some light may be shed on factors determining this distribution by consideration of the greater size of *Hydrobia* within *Spartina* at Site B, both in June and September.

Before discussing these factors, it is again necessary to consider the importance of movement as a determining influence in the distribution. Hydrobia can often be observed moving over the mud surface at low water. Newell (1962) described a cycle of behaviour at Whitstable, Kent, which is closely linked with the tidal cycle. After the tide receded, animals crawled on the surface before burrowing for several hours, resurfacing and launching themselves on the surface film of water between ripple marks and then floating on the incoming tide. When stranded by the ebbing tide, the animals browsed and orientated themselves to bring them back approximately to the place where they started. Anderson (1971) reported large scale movements on the Ythan, and mentioned one mass exodus by an upstream population which floated down on the ebb tide and returned on the flow. He concluded that this was an important dispersive mechanism in the life cycle. Vader (1964), working in the Netherlands, claimed that Hydrobia browsed on the mud surface at High Water and burrowed when the tide receded. He found no evidence of the inherent cycle of floating behaviour suggested by Newell. Wood (1972) working at Budle Bay, found that marked animals dispersed more quickly from open mud than from areas of Enteromorpha. In view of this body of supporting evidence, I conclude that the movement detected at Site B was natural and not experimentally induced. However, the degree of movement detected there (approximately ½ m in 19 tides) is not large enough to account for major changes in distribution of Hydrobia populations throughout the season. My observations did not reveal large-scale floating during the high water period. As for Corophium, I conclude that my distribution results for Hydrobia represent a relatively permanent seasonal distribution of animals rather than a dynamic balance involving movement of a majority of animals between *Spartina* and the open mud. The greater mean size of animals within *Spartina* at Site B supports this since if there was a continual exchange of animals, one would expect mean lengths to be the same.

As for *Corophium*, comparisons to be made, and indications of their reliability, are summarised in Table 32 (p.118).

Although Newell (1965) found the greatest densities of *Hydrobia* within the finest deposits, this was not the case at Lindisfarne. Within the *Spartina* sward at Site B, where the highest silt contents were found, *Hydrobia* was virtually absent from the first 60 m of sward, and beyond this densities were slightly less than those outside, both in summer and winter. My study of habitat selection in *Hydrobia* indicated that above a 50% silt content, there was an inverse relationship between density and silt content. Since all stations with silt contents greater than 50% occurred within *Spartina*, these high silt contents may account for the absence of *Hydrobia* from the first 60 m of sward. The general absence of *Hydrobia* from the upper sward at Site B could have resulted from the very shallow R.P.D. This seems unlikely, however, since *Hydrobia* was present at Station BS 90 in the summer when the R.P.D. was only 3 mm below the surface. In any case, one would not expect *Hydrobia* to be as affected by depth of R.P.D. as *Corophium* since *Hydrobia* does not burrow so deeply or for so much of the low tide period as the latter. Observations of the incoming tide indicated that of the three transects at Site B, the upper part of BS was the last to be covered. *Spartina* may thus have raised the sediment within the first 60 m of the sward to a level equivalent to that of the first 30 m of transects BC and BM where *Hydrobia* was scarce or absent also. Stopford (1951) found that *Hydrobia* began to die after 4 days in dryness and this may account for its absence from the shore zone which is reached only by the higher spring tides.

Although after a few tides, the degree of movement by Hydrobia differed in areas of Spartina and open mud, both in distance covered and percentage remaining in original area, after 19 tides results were similar in the two areas. Thus the evidence does not indicate whether Hydrobia within Spartina move more or less than those outside.

At Site E Hydrobia densities increased in direct proportion to silt content, as found by Newell (1965). Within the Spartina, the silt contents, although on average higher than those outside, were not significantly so. Nevertheless, it is possible that higher bacterial populations within the Spartina, together with accumulation of filamentous green algae around the Spartina clumps, may have attracted the Hydrobia (Wood 1972).

Autumn mortality may have been less severe than in Corophium, since the differences between summer and winter densities and distributions of Hydrobia were less marked. At the end of the season, the absence of a difference between Hydrobia densities inside and outside three of the four exclosures could partly be explained by a lack of predation, but free movement in and out of the exclosures is a viable alternative explanation. During Spring 1973 at Site B, the growth of filamentous green algae within the exclosure may have attracted Hydrobia, as demonstrated by Wood (1972). Nevertheless, predation of Hydrobia did take place since they were discovered in the gizzards of Redshank from both Budle Bay (Site B) and Elwick (Sites E and W). However, results suggest that the impact of bird predation on Hydrobia numbers is small.

The larger *Hydrobia* found within *Spartina* could reflect lower mortality within the *Spartina* or a net movement of older animals into the *Spartina*. There is no evidence either that older animals move more than younger ones or that any net movement into the *Spartina* took place. Predation by Redshank over a period of time, albeit at a low rate, could account for the difference in *Hydrobia* size between the *Spartina* and open mud. It is possible that mortality from climatic factors would act differentially on *Hydrobia* in the two habitats although there is no evidence to support this. At Site E, the lack of significant size difference may reflect the small sample size from the open mud or equivalent predation pressure inside and outside the *Spartina*. Since no bird studies were made at Site E, it is difficult to draw conclusions. However, the less dense *Spartina* with its intervening patches of open mud may have allowed shorebirds to penetrate further into the areas of *Spartina* than at Site B.

(3) Shorebirds feed as the tide ebbs and flows, many on open areas where they can see predators approaching and where they can flock. Most rely on visual cues for detecting their prey and therefore concentrate where the prey is active or visible, often near the tide edge. Species which feed in *Spartina* or on open mud at high levels may do so (a) because they have to feed throughout the tidal cycle in order to obtain sufficient food to balance energy loss, or (b) because they choose to feed among the clumps.

(a) Goss-Custard (1969) found that Redshank on the River Ythan fed for more than 96% of the available daylight hours during the period from October to February. Evans (1974a, 1974b) obtained similar results for Redshank, Dunlin and Grey Plover at Teesmouth. These findings are reflected in the relatively high indices of occurrence and feeding for Redshank and Dunlin at Sites B and W. In the case of the Grey Plover at Lindisfarne, the low indices of feeding at Sites B and W probably reflect the low winter numbers (Table 33) with few birds scattered over a wide area. (The other species with low winter numbers is the Turnstone which is more characteristic of rocky shores than the sand and mudflats at Lindisfarne.) Hence it can be concluded that these two species feed among the Spartina when lower areas are flooded, out of necessity.

(b) As well as needing to feed among Spartina either side of high water, many Redshank also fed there during the low tide period when other areas were available (Figs. 56 and 57). In contrast, Dunlin at Site B were absent from the Spartina during the low water period. Although this was not so evident at Site W, it is probable that a more lengthy observation programme there would also have indicated peaks of Dunlin occurrence immediately before and after High Water. This behaviour indicates that Dunlin prefer to feed downshore of the Spartina when the tide has receded enough. Some Dunlin were observed feeding along the tidal edge where prey are often more active and hence easily detected. However, the rest fed on open mud between the Spartina zone and the tidal edge. This habit of avoiding the Spartina zone whenever possible may be associated with the flocking habit of Dunlin, also found in many other shorebird species, except Redshank and Grey Plover (see below).

Reasons for flocking in shorebirds are not fully understood, but it seems likely that it acts as an anti-predator device and may stimulate individuals within the flock to feed more efficiently. At Lindisfarne, Smith and Evans (1973) found that solitary Bar-tailed

TABLE 33

Maximum winter counts of shorebirds at Lindisfarne

Species	1972/73	1973/74
Redshank	1300	1200
Dunlin	15500	22000
Curlew	1700	1150
Bar-tailed Godwit	3000	6700
Oystercatcher	1830	1670
Grey Plover	210	200
Shelduck	600	700
Turnstone	270	180
Teal	320	520
Knot	11000	5500

Godwits were less successful feeders than birds feeding in flocks and often spent more time standing in an upright, alert position. The presence of Spartina clearly makes flocking difficult or impossible by preventing the visual communication necessary to maintain the structure of the flock. Thus the Dunlin, which feeds in tightly packed flocks, is more likely to prefer feeding on the open mud than among the Spartina. This probably explains the general absence of other flocking species (Curlew, Bar-tailed Godwit, Oystercatcher and Knot) from the Spartina. In addition, their preferred diets (Table 34) are found either in comparable or greater numbers below the Spartina zone, and sometimes exclusively so. Also, they do not normally have to feed throughout the tidal cycle.

In contrast, Redshank and Grey Plover are usually non-flocking birds and therefore their feeding is unlikely to be affected adversely by the presence of Spartina. Moreover, when Redshank are territorial, as was sometimes observed at Lindisfarne, Spartina clumps may reduce visual contact between individuals, thus preventing disputes over territory and allowing more time for feeding. In addition, analysis of gut contents (Table 28) indicated that the preferred prey species of some Redshank at Lindisfarne came from the upper shore zone, and of these invertebrates, four were found mostly within Spartina. Thus a considerable proportion of the Lindisfarne Redshank population (between 28.4% and 62.4%) are utilising areas which are largely ignored by most other species of shorebirds.

The preferred diet (Table 34) and non-flocking behaviour of the Grey Plover suggests that, as well as having to feed among the Spartina either side of high water, they may choose also to feed there

TABLE 34

Preferred diets of shorebirds

Species	Diet	Location	Reference
Redshank	*Corophium*, *Hydrobia*, *Littorina*, *Nereis*, *Carcinus*, *Mytilus*.	Lindisfarne	See p. 95.
"	*Corophium*	River Ythan	Goss-Custard (1969)
"	*Crangon*, *Carcinus*, shrimps, small cockles, *Macoma*, *Hydrobia*.	The Wash	Goss-Custard & Jones (1975)
Curlew	*Arenicola*	Lindisfarne	P.C. Smith (pers. comm.)
"	*Arenicola*, *Lanice*, *Carcinus*.	The Wash	Goss-Custard & Jones (1975)
Bar-tailed Godwit	*Arenicola*	Lindisfarne	Smith & Evans (1973)
Oystercatcher	*Cardium edule*		Drinnan (1957)
"	*Mytilus edulis*		Norton Griffiths (1966)
Grey Plover	*Nereis*, *Scoloplos*	Lindisfarne	M. Pienkowski (pers. comm.)
Turnstone	Gastropods, amphipods, isopods and decapods	Morecambe Bay	Prater (1972b)
Knot	*Macoma*	" "	Prater (1972a)
Shelduck	Anything obtainable by sieving soft mud, especially oligochaetes.	Teesmouth	P.R. Evans (pers. comm.)
Teal	*Salicornia* and seeds of other common saltmarsh plants excluding *Spartina* and *Halimione portulacoides*.		Olney (1963)

during the low water period. Evidence for this is sparse because of the small number of birds involved. However, individuals were observed occasionally outside the study areas feeding among *Spartina* clumps, and it may be concluded that the Grey Plover has a greater degree of association with *Spartina* than many of the shorebird species, particularly the flocking ones.

The degree of association between Shelduck and *Spartina* is difficult to evaluate, as are the factors controlling the duck's distribution. Despite the low Index of Feeding at Site B and its absence from Site W, Shelduck were observed feeding both on the seaward side of *Spartina*, and occasionally among the clumps. Since Shelduck feed by sieving through soft mud, it is possible that they may be attracted sometimes by the higher silt/clay content associated with *Spartina*, although further evidence would be needed to confirm this.

The preferred diet of Teal (Table 34) indicates that it needs to feed high up the shore and hence at Lindisfarne is found either among or on the landward edge of *Spartina*. The low Index of Occurrence at Site B reflects the habit of most Teal at Budle Bay to collect further west along Ross Low in the corner of the Bay (Fig. 2).

Mallard and Lapwing, the two remaining species of shorebird observed during the study, used the *Spartina* zone only for roosting. In this context, it should be remembered that clumps of *Spartina* can provide shelter for shorebirds in harsh weather, and at Lindisfarne were used in this way by Redshank during gales.

(4) Further spread of Spartina at Lindisfarne seems inevitable unless some preventative action is taken. However, the extent and form of future colonisation is less easy to predict. It seems certain that the few remaining areas of open mud at the upper shore level will be colonised eventually, although not necessarily by extensive swards. In exposed areas with coarse sediment (e.g. Site E) growth is likely to be less vigorous, with more patches of open mud remaining than in sheltered areas. In the long term extensive swards may become affected by 'die-back' although patches of open mud formed in this way are likely to have similar sediment characteristics, and hence similar faunas, to the rest of the sward.

Further spread of Spartina at Lindisfarne could affect the shorebirds in three ways. Firstly, it may reduce the area of Zostera available to Wigeon, Brent Geese and Whooper Swans. I did not observe these species feeding in my study areas, although P.C. Smith (pers. comm.) noted Wigeon feeding for between 8 - 13% of the daylight hours within Spartina swards near Fenham Mill during the winter, particularly in December. Nevertheless, encroachment of Spartina into the landward end of the Zostera beds may seriously affect these species, especially as several fungal infections of Zostera have been reported at Lindisfarne. Ranwell and Downing (1959) noted that Spartina reduced the area of upper shore zone saltmarsh plants on the South Coast and hence restricted the diet of Brent Geese there. At Lindisfarne Brent Geese feed mainly out on the open flats and it is doubtful whether Spartina would affect the Geese in this way, although it may have done so in the past. Use of Spartina might well be greater if wildfowling were restricted. Olney (1963) concluded that reduction of *Spartina* would be necessary to increase the food of the Teal and this would seem to be the situation at Lindisfarne.

Secondly, further spread of *Spartina* along the shore could lead ultimately to colonisation of all the upper shore zone at Lindisfarne, thus reducing the feeding time available to shorebirds. The worst affected will be those flocking species which need to feed for most of the tidal cycle (e.g. Dunlin), particularly during short daylight hours and harsh climatic conditions. As there is a downshore limit to the spread of *Spartina*, other flocking species which feed only for part of the tidal cycle are unlikely to be so seriously affected.

Non-flocking species (e.g. Redshank, Grey Plover) are unlikely to be seriously affected if remaining areas of open mud along the upper shore are colonised by *Spartina* clumps. However, if extensive swards develop, the Grey Plover may have its feeding area seriously reduced. The Redshank, though, with its wide range of recorded prey items (Table 34), may be able to supplement its diet by feeding elsewhere, e.g. on the fields at High Water (which Grey Plover will never do) or further down the shore.

Finally, in areas of coarse sediment, further spread of *Spartina* may benefit shorebirds initially by increasing the numbers and diversity of potential prey species amongst the *Spartina* clumps, as at Site E.

APPENDIX I

Methods of sediment analysis

i. Estimation of organic carbon

a. Walkley Black wet oxidation method.

Outline (Full details given in Morgans 1956)

Oven-dried sediment is oxidised by potassium dichromate in the presence of concentrated sulphuric acid. No heating is employed. The chromic sulphate formed is titrated against ferrous sulphate in the presence of phosphoric acid, using diphenylamine indicator.

N.B. In my study silver sulphate was dissolved in the sulphuric acid to precipitate any chlorides present in the sediment.

b. Tinsley-modified Walkley Black method.

Outline (Full details given in Tinsley 1950)

After addition of the potassium dichromate, sulphuric acid and phosphoric acid to the oven-dried sediment, the mixture is heated under a reflux condenser for one hour and then allowed to cool. Titration is as described for the normal Walkley Black method.

ii. Estimation of nitrogen using the Kjeldahl semi--micro method.

Outline (Full details given in Mann and Saunders 1960).

Oven-dried sediment is digested in a Kjeldahl flask over a micro-burner for 50 minutes, using concentrated sulphuric acid and a catalyst consisting of potassium sulphate and selenium powder. After cooling, the flask is attached to steam distillation apparatus. A mixture of sodium hydroxide and sodium sulphide is then added to the digestion mixture to release the ammonia. The ammonia is distilled into a saturated boric acid solution which is then titrated against hydrochloric acid using methyl-red/methylene-blue indicator.

A blank estimation is made to check purity of the reagent using A.R. glucose in place of the sediment. The volume of hydrochloric acid used is then subtracted from the titres obtained in the sediment analysis.

iii. Estimation of silt/clay fraction of sediment

Outline (Full details given in Holme and McIntyre 1971).

Oven-dried sediment is weighed and placed in a beaker with tap water and sodium hexametaphosphate. The mixture is stirred and allowed to stand overnight before washing through a 62μ sieve. The residue is dried at 100°C and reweighed.

APPENDIX 2

Results from winter invertebrate sampling programme

1. Site B.

		Species							
Sample		Corophium	Hydro-bia	Macoma	Nereis	Scolo-plos	Litt-orina	Car-cinus	Areni-cola
BS 0	1.	6	0	0	1	0	0	0	0
"	2.	8	0	0	1	0	0	0	0
"	3.	7	0	0	1	0	0	0	0
"	4.	20	0	0	0	0	0	0	0
BS 30	1.	31	1	0	0	0	0	1	0
"	2.	11	0	0	0	0	0	1	0
"	3.	15	0	0	0	0	0	0	0
"	4.	6	0	0	0	0	0	0	0
BS 60	1.	0	0	0	0	0	1	0	0
"	2.	0	0	0	0	0	0	0	0
"	3.	0	0	0	0	0	0	1	0
"	4.	0	0	0	0	0	0	1	0
BS 90	1.	0	2	0	0	0	1	0	0
"	2.	0	3	0	0	0	0	0	0
"	3.	0	7	0	0	0	0	0	0
"	4.	0	6	0	0	0	0	0	0
BS 150	1.	0	15	0	0	0	0	0	1
"	2.	0	10	0	0	0	0	0	0
"	3.	0	15	0	0	0	0	0	0
"	4.	0	22	0	0	0	0	0	0
BC 0	1.	84	0	0	2	0	0	0	0
"	2.	106	0	0	4	0	0	0	0
"	3.	83	0	0	1	0	0	0	0
"	4.	122	0	0	0	0	0	0	0
BC 30	1.	52	0	0	2	0	0	1	0
"	2.	42	1	0	1	0	0	1	0
"	3.	75	2	0	0	0	0	0	0
"	4.	65	1	1	0	0	0	0	0
BC 90	1.	14	26	0	2	0	1	0	0
"	2.	21	20	0	0	0	1	0	0
"	3.	87	6	0	0	0	0	0	0
"	4.	5	8	0	0	0	0	0	0
BC 150	1.	0	11	0	0	0	1	1	0
"	2.	0	11	0	0	0	1	0	0
"	3.	0	4	1	0	0	3	0	0
"	4.	0	5	1	0	0	0	0	0
BC 210	1.	0	9	0	0	0	1	0	0
"	2.	0	3	0	0	0	0	0	0
"	3.	0	13	1	0	0	0	0	0
"	4.	0	20	2	0	0	0	0	0
BM 0	1.	27	1	0	1	0	0	0	1
"	2.	62	0	0	1	0	0	0	0
"	3.	60	0	0	0	0	0	0	0
"	4.	39	0	0	0	0	0	0	0
BM 30	1.	3	4	0	0	0	0	0	0
"	2.	2	4	0	0	0	0	0	0
"	3.	6	14	0	0	0	0	0	2
"	4.	3	11	0	0	0	0	0	1
BM 90	1.	1	50	0	0	1	0	0	0
"	2.	1	50	2	0	0	0	0	0
"	3.	1	45	1	1	0	0	0	0
"	4.	0	41	0	1	0	0	0	0
BM 150	1.	0	14	0	0	12	1	0	0
"	2.	0	15	1	0	4	0	0	0
"	3.	0	20	1	0	6	0	0	0
"	4.	0	19	0	0	11	0	0	0
BM 210	1.	0	9	2	0	12	0	0	0
"	2.	0	8	0	0	13	0	0	0
"	3.	0	10	2	0	18	0	0	0
"	4.	0	15	4	0	11	0	0	0

ii. Site E.

Sample		Hydrobia	Macoma	Scoloplos	Littorina	Carcinus	Arenicola
ES 30	1.	3	0	0	0	0	0
"	2.	2	0	0	0	0	0
"	3.	2	1	0	0	0	0
"	4.	0	0	0	0	0	1
ES 60	1.	13	0	0	0	0	0
"	2.	6	0	0	0	0	0
"	3.	13	0	0	2	2	1
"	4.	56	0	0	1	2	1
ES 90	1.	23	1	1	0	0	0
"	2.	20	0	4	0	0	0
"	3.	12	0	2	0	0	1
"	4.	27	1	1	0	0	1
ES 150	1.	4	0	0	0	0	0
"	2.	0	0	0	0	0	0
"	3.	1	0	0	2	0	0
"	4.	0	0	0	0	0	0
ES 210	1.	29	2	0	1	0	0
"	2.	12	2	2	3	0	0
"	3.	10	0	2	1	0	0
"	4.	29	0	2	0	0	0
EM 30	1.	1	1	0	0	0	0
"	2.	1	1	0	0	0	1
"	3.	1	0	0	0	0	1
"	4.	1	0	0	0	0	0
EM 60	1.	0	0	1	0	0	0
"	2.	0	0	5	0	0	0
"	3.	0	0	3	0	0	0
"	4.	0	0	0	0	0	0
EM 90	1.	1	1	16	0	0	0
"	2.	1	0	6	0	0	0
"	3.	0	0	9	0	0	0
"	4.	0	0	0	0	0	0
EM 150	1.	0	1	5	0	0	0
"	2.	0	0	18	0	0	0
"	3.	0	0	6	0	0	0
"	4.	0	0	0	0	0	0
EM 210	1.	1	1	18	0	0	0
	2.	3	0	8	0	0	0
"	3.	1	0	13	0	0	0
"	4.	0	0	18	0	0	0
"							

APPENDIX 3

i. Sample weights (mgm) for Corophium volutator at Site B. Samples from within Spartina are indicated (*) and samples sizes (n) are given.

		Size class (mm)							
	Sample	2 - 2.9	3 - 3.9	4 - 4.9	5 - 5.9	6 - 6.9	7 - 7.9	8 - 8.9	9 - 9.9
Winter 1973/74	BS 0	0.045 n = 10	0.098 n = 8	0.434 n = 6	0.348 n = 3				
	BS 30*	0.061 n = 3	0.178 n = 21	0.368 n = 18	0.676 n = 9				
	BC 0	0.039 n = 70	0.082 n = 136	0.207 n = 44	0.383 n = 25	0.519 n = 6			
	BC 30	0.053 n = 35	0.131 n = 42	0.260 n = 21	0.507 n = 11	0.796 n = 4			
	BC 90*	0.058 n = 13	0.127 n = 39	0.272 n = 46	0.481 n = 15	0.655 n = 3	1.111 n = 2		
	BM 0	0.058 n = 31	0.136 n = 80	0.298 n = 33	0.432 n = 3	0.527 n = 1			
Summer 1974	BS 0			0.400 n = 60	0.718 n = 85	1.187 n = 48	1.812 n = 33	2.400 n = 4	
	BS 30*				0.725 n = 8	1.436 n = 11	2.264 n = 39	3.100 n = 23	5.975 n = 4
	BC 30			0.436 n = 44	0.748 n = 59	1.230 n = 88	1.727 n = 64	3.340 n = 5	2.200 n = 1
	BC 60				0.475 n = 4	1.495 n = 17	2.101 n = 11		
	BM 30			0.390 n = 10	0.834 n = 33	1.362 n = 68	2.035 n = 54	3.080 n = 5	
	BM 60				1.044 n = 30	1.680 n = 60	2.332 n = 60	3.600 n = 3	

ii. Results of *Corophium* response experiment in the field.

a. *Spartina* (transect BS)

Minutes after intro-duction	Number of *Corophium* observed swimming	No. of observations
1 - 4	19,24,1,2,20,19,14,19,18,10,8,13,9,4,3.	15
5 - 8	24,0,0,14,10,7,1,1.	8
9 - 12	17,3,3.	3
13 - 16	22,0,2,1.	4
17 - 20	0,1,0.	3

b. Open mud (transect BM)

Minutes after intro-duction	Number of *Corophium* observed swimming	No. of observations
1 - 4	9,11,5,1.	4
5 - 8	8,9,0.	3
9 - 12	10,0.	2
13 - 16	-	0
17 - 20	0.	1

APPENDIX 4

i. Sample weights (mgm) for Hydrobia ulvae at Sites B and E in December 1973. Sample sizes (n) are given.

Transect	Size class (mm) 2 - 2.9	3 - 3.9	4 - 4.9	5 - 5.9	6 - 6.9	7 - 7.9	8 - 8.9	9 - 9.9
BS		0.798 n = 11	0.982 n = 36	1.408 n = 26	1.745 n = 2	2.535 n = 2		
BC		0.568 n = 9	0.934 n = 22	1.251 n = 37	1.530 n = 4	2.910 n = 1		
			0.880 n = 22					
			0.950 n = 28					
BM		0.433 n = 39	0.779 n = 20	1.321 n = 24	1.793 n = 3	1.720 n = 2		
		0.597 n = 33	1.030 n = 20					
ES	0.080 n = 5	0.550 n = 26	0.908 n = 20	1.848 n = 31	4.208 n = 6			
		0.790 n = 28						
FM		0.540 n = 3	0.900 n = 6	0.770 n = 1				

APPENDIX 5

i. Observations of shorebird species associated with <u>Spartina</u> 1973/74.

Redshank - Site B.

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding
1	Morning		-	-	Morning		-	-	Morning	
	-	-	-	-			-	-		
	-	-	-	-			-	-		
	-	-	-	-			-	-		
2	3	1	-	-			1	-	1	-
	7	6	-	-	-	-	10	10		
	7	6	-	-	-	-	13	12	3	3
	8	7	1	1	-	-	5	5	10	8
3	3	3	-	-	-	-	7	7	12	12
	2	2	1	1	-	-	13	12	5	4
	2	2	2	2	-	-			3	3
	2	2	2	2	-	-	13	12	4	3
4	-	-	4	4	-	-	20	20	2	2
	7	7	Evening		-	-	5	4	8	8
	-	-			-	-	7	7	3	1
	-	-			-	-	9	9	4	4
5	1	1			-	-	7	6	4	2
	1	1			-	-	1	1	4	2
	3	2			-	-	5	5	1	1
	-	-			-	-	5	3	6	5
6	1	1			-	-	4	4	7	7
	-	-			-	-	Evening		3	2
	-	-			-	-			12	11
	2	1			-	-			8	7

Redshank - Site B (continued)

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding
7	-	-			-	-			6	6
	1	1	Morning		-	-	Morning		7	7
	3	3	2	2	-	-	1	1		
	2	2	4	3	-	-				
8	1	1	2	2	-	-	2	2		
	2	1	4	-	-	-	1	-	8	8
	-	-	1	1	-	-	2	2	4	3
	1	-	5	5	-	-	6	5	7	6
9	1	1	3	3	-	-			7	6
	1	1	7	7			Disturbance		4	4
	1	1	-	-					-	-
	-	-	3	3			3	3	10	8
10	1	-	1	-			12	12	16	8
	-	-	2	2			3	3	-	-
	-	-	2	2			9	8	2	2
	-	-	3	3			9	7	4	3
11	1	1	2	2			9	5	6	5
	3	1	2	2			10	10	2	1
	1	1	4	4			10	10	3	2
	2	2	2	1			7	5	17	14
12	3	3	-	-			16	16	14	11
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	Evening				Evening				Evening	

Dunlin - Site B.

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding
1	Morning									
	-	-	-	-			-	-		
	-	-	-	-			-	-		
	-	-	-	-			-	-	Morning	
	-	-	-	-	Morning		-	-		
2	-	-	-	-			-	-	-	-
	4	-	-	-	-	-	4	4		
	1	1	-	-	-	-	4	4	-	-
	-	-	-	-	-	-	65	65	-	-
3	-	-	4	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-			-	-
	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-
	-	-	Evening		-	-	-	-	-	-
	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
5	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
6	-	-			-	-	-	-	-	-
	-	-			-	-	Evening		-	-
	-	-			-	-			-	-
	-	-			-	-			-	-

Dunlin - Site B (continued)

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding
7	-	-			-	-			-	-
	-	-	Morning		-	-			-	-
	-	-	-	-	-	-	Morning			
	-	-	-	-	-	-	-	-		
8	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-			-	-
	-	-	-	-			Disturbance		-	-
	-	-	-	-					-	-
	-	-	-	-			13	13	-	-
10	-	-	-	-			10	10	-	-
	-	-	-	-			-	-	-	-
	-	-	3	3			4	4	-	-
	-	-	-	-			-	-	-	-
11	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	35	35			13	13	-	-
	-	-	58	52			-	-	-	-
12	-	-	-	-			6	6	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-	Evening		-	-	-	-
	Evening								Evening	

<u>Curlew - Site B.</u>

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing
1	Morning									
	-	-	-	-	Morning		-	-		
	-	-	-	-			-	-	Morning	
	-	-	-	-			-	-		
	-	-	-	-			-	-		
2	1	-	-	-			-	-	-	-
	1	-	-	-	-	-	-	-		
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	1	-	-	-
3	-	-	-	-	1	-	-	-	-	-
	-	-	-	-	1	-	-	-	-	-
	1	1	2	-	1	-	-	-	-	-
	-	-	1	1	1	-	-	-	-	-
4	-	-	-	-	1	-	-	-	-	-
	-	-	Evening		-	-	-	-	-	-
	-	-			1	-	-	-	-	-
	-	-			-	-	-	-	-	-
5	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
	-	-			1	-	-	-	-	-
	-	-			2	-	-	-	-	-
6	-	-			1	-	-	-	-	-
	-	-			-	-	Evening		-	-
	-	-			-	-			1	1
	-	-			-	-			-	-

Curlew - Site B (continued)

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing
7	-	-			-	-			-	-
	-	-	Morning		-	-			-	-
	-	-	-	-	-	-	Morning			
	-	-	-	-	-	-	-	-		
8	1	1	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-			-	-
	-	-	-	-			Disturbance		-	-
	-	-	1	-					-	-
	1	-	-	-			-	-	-	-
10	1	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	1	1			-	-	-	-
11	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	2	1	-	-			-	-	-	-
	1	1	-	-			-	-	-	-
12	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	Evening				Evening				Evening	

Bar-tailed Godwit - Site B.

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding
1	Morning-		-	-	Morning		-	-	Morning	
	-	-	-	-			-	-		
	-	-	-	-			-	-		
	-	-	-	-			-	-		
2	-	-	-	-			-	-	-	-
	-	-	-	-	-	-	2	2		
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-	2	2
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-			-	-
	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-
	-	-	Evening		-	-	-	-	-	-
	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
5	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
6	-	-			-	-	-	-	-	-
	-	-			-	-	Evening		-	-
	-	-			-	-			-	-
	-	-			-	-			14	14

Bar-tailed Godwit - Site B (continued)

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding
7	-	-			-	-			9	9
	-	-	Morning		-	-	Morning		-	-
	-	-	-	-	-	-	-	-		
	-	-	-	-	-	-				
8	-	-	-	-	-	-	-	-		
	1	1	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-	Disturbance		-	-
	-	-	-	-					-	-
	-	-	-	-					-	-
	-	-	-	-			-	-	-	-
10	-	-	-	-			-	-	-	-
	1	1	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
11	-	-	1	-			-	-	-	-
	-	-	2	2			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	3	3
12	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	Evening				Evening				Evening	

Oystercatcher - Site B.

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding
1	Morning		-	-	Morning		-	-	Morning	
	-	-	-	-			-	-		
	-	-	-	-			-	-		
	-	-	-	-			-	-		
2	-	-	-	-			-	-	-	-
	5	4	-	-	-	-	2	2		
	6	1	-	-	-	-	-	-	-	-
	3	3	-	-	-	-	1	1	3	-
3	1	1	-	-	-	-	-	-	2	2
	-	-	3	2	-	-	-	-	3	3
	-	-	2	2	-	-			-	-
	-	-	-	-	-	-	-	-	2	2
4	-	-	-	-	-	-	-	-	1	1
	-	-	Evening		-	-	-	-	2	2
	-	-			-	-	-	-	1	1
	-	-			-	-	-	-	-	-
5	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
6	-	-			-	-	-	-	-	-
	-	-			-	-	Evening		-	-
	-	-			-	-			-	-
	-	-			-	-			-	-

Oystercatcher - Site B (continued)

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing
7	-	-			-	-			-	-
	-	-	Morning		-	-				
	-	-	-	-	-	-	Morning			
	-	-	-	-	-	-	-	-		
8	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-			-	-
	-	-	-	-			Disturb-ance			
	-	-	-	-					-	-
	-	-	-	-			-	-	-	-
10	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
11	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	2	2
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-	Evening		-	-	-	-
	Evening								Evening	

<u>Minor Species - Site B.</u>

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing
1	Morning		-	-	Morning		-	-	Morning	
	-	-	-	-			-	-		
	-	-	-	-			-	-		
	-	-	-	-			-	-		
2	-	-	-	-			-	-	-	-
	-	-	-	-	-	-	1S	1S		
	1S	1S	-	-	-	-	-	-	-	-
	2S	2S	-	-	-	-	-	-	3B	-
3	1S	1S	-	-	-	-	-	-	3B	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-			2M	-
	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-
	-	-	Evening		-	-	-	-	1Tu, 1GB	1Tu
	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	1Tu	1Tu
5	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
	-	-			-	-	-	-	-	-
6	-	-			-	-	-	-	-	-
	-	-			-	-	Evening		-	-
	-	-			-	-			-	-
	-	-			-	-			2S	2S

For key to species see overleaf.

Minor Species - Site B (continued)

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding
7	-	-			-	-			-	-
	-	-	Morning		-	-			-	-
	-	-	-	-	-	-	Morning			
	-	-	-	-	-	-	-	-		
8	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-			-	-
	-	-	-	-			Disturbance		-	-
	-	-	1Gr	1Gr					-	-
	-	-	-	-			-	-	-	-
10	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
11	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	1Gr	1Gr			-	-	2T	1T
	1Gr	1Gr	1Gr	1Gr			-	-	-	-
12	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	-	-	-	-			-	-	-	-
	Evening				Evening				Evening	

S = Shelduck M = Mallard B = Blackheaded Gull

Tu = Turnstone Gr = Grey Plover T = Teal GB = Great Black-backed Gull

Redshank - Site W.

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing
1	Morning									
	-	-	-	-	Morning		-	-	Morning	
	-	-	-	-						
	-	-	-	-						
	-	-	-	-			Fog			
2			-	-						
	1	-								
			-	-						
	1	1	1	-	-	-				
3	2	2	8	-	-	-	2	1		
			-	-	2	2			1	-
	8	5	2	-	1	1	2	1		
	2	1	1	-	3	3	2	1	3	1
4	-	-	-	-	-	-	5	4	-	-
	-	-	Evening		-	-	8	7	2	1
	-	-			1	1			3	3
	-	-			-	-	Fog			
5	4	3			-	-			5	4
	-	-			3	3			-	-
	-	-			1	1			-	-
	-	-			-	-			-	-
6					1	1	Evening		-	-
	4	4			1	-			1	-
	-	-			-	-			1	1
	-	-			-	-				

Redshank - Site W (continued)

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing
7	-	-			-	-			3	1
	2	2	Morning		1	1			1	-
	1	1	-	-	-	-				
	-	-	-	-	1	-	Morning			
8	-	-			2	-			5	4
	-	-	-	-	-	-			5	5
	2	1	-	-	-	-			8	7
	3	2	-	-	3	3			-	-
9	1	1			2	1			-	-
	-	-			3	1			3	2
	2	1	-	-	4	4	Fog		2	1
	2	2	-	-	2	2			4	3
10	1	1	-	-	1	1			3	3
	-	-	-	-	-	-			4	4
	1	1	-	-	1	1			4	4
	-	-	-	-	-	-			5	4
11	-	-	-	-					6	6
	1	1	8	5						
	-	-	-	-					4	3
	1	1	3	-					6	6
12	-	-	-	-					2	2
	-	-	-	-					-	-
	-	-	-	-						
	-	-	-	-						
	Evening				Evening				Evening	

Dunlin - Site W.

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing
1	Morning									
	-	-	-	-	Morning		-	-	Morning	
	-	-	-	-						
	-	-	-	-						
	-	-	-	-			Fog			
2			-	-						
	-	-								
			-	-						
	-	-	-	-	-	-				
3	66	65	-	-	-	-	-	-		
			-	-	250	250			-	-
	3	2	-	-	-	-	-	-		
	53	52	-	-	-	-	-	-	-	-
4	2	2	-	-	-	-	-	-	-	-
	4	4	Evening		-	-	4	4	-	-
	4	2			-	-			-	-
	-	-			-	-				
5	-	-			-	-			-	-
	11	10			-	-			-	-
	-	-			-	-			-	-
	-	-			-	-	Fog		-	-
6					1	1			-	-
	-	-			80	80			-	-
	-	-			-	-			-	-
	-	-			22	22	Evening			

Dunlin - Site W (continued)

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing
7	-	-			-	-			-	-
	-	-	Morning		-	-			-	-
	-	-	-	-	-	-				
	-	-	-	-	-	-	Morning			
8	18	16			-	-			-	-
	17	17	-	-	-	-			-	-
	-	-	-	-	-	-			-	-
	14	14	-	-	-	-			-	-
9	14	9			-	-	Fog		-	-
	23	23			-	-			-	-
	2	2	-	-	-	-			-	-
	73	70	-	-	-	-			-	-
10	-	-	-	-	-	-			-	-
	-	-	-	-	-	-			-	-
	-	-	6	6	-	-			-	-
	2	2	20	20	-	-			-	-
11	8	8	-	-					-	-
	10	10	-	-						
	1	1	-	-					-	-
	1	1	100	100					-	-
12	-	-	-	-					-	-
	-	-	-	-					-	-
	-	-	-	-						
	-	-	-	-						
	Evening				Evening				Evening	

Grey Plover - Site W.

Hours after High water	31/10/73 Pres-ent	31/10/73 Feed-ing	8/11/73 Pres-ent	8/11/73 Feed-ing	30/1/74 Pres-ent	30/1/74 Feed-ing	3/4/74 Pres-ent	3/4/74 Feed-ing	11/4/74 Pres-ent	11/4/74 Feed-ing
	Numbers observed in study area									
1	Morning									
	-	-	-	-	Morning		-	-	Morning	
	-	-	-	-						
	-	-	-	-						
	-	-	-	-			Fog			
2			-	-						
	2	2								
			-	-						
	-	-	-	-	-	-				
3	1	1	-	-	-	-	-	-		
			-	-	-	-			-	-
	5	4	-	-	-	-	-	-		
	-	-	-	-	-	-	-	-	-	-
4	1	1	-	-	-	-	-	-	-	-
	-	-	Evening		-	-	-	-	-	-
	-	-			-	-	Fog			
	1	1			-	-				
5	-	-			-	-			-	-
	1	1			-	-			-	-
	1	1			-	-			-	-
	-	-			-	-			-	-
6					-	-			-	-
	-	-			-	-			-	-
	1	1			-	-	Evening		-	-
	-	-			-	-				

Grey Plover - Site W (continued)

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing	Pres-ent	Feed-ing
7	-	-			-	-			-	-
	-	-	Morning		-	-			-	-
	-	-	-	-	-	-	Morning			
	1	1	-	-	-	-				
8	1	1			-	-			-	-
	2	2	-	-	-	-			-	-
	-	-	-	-	-	-			-	-
	1	1	-	-	-	-			-	-
9	1	1			-	-			-	-
	1	1			-	-			-	-
	1	1	-	-	-	-	Fog		-	-
	-	-	-	-	-	-			-	-
10	-	-	-	-	-	-			-	-
	-	-	-	-	-	-			-	-
	-	-	-	-	-	-			-	-
	-	-	-	-	-	-			-	-
11	-	-	-	-					-	-
	1	1	-	-						
	1	1	-	-					-	-
	1	1	-	-					-	-
12	-	-	-	-					-	-
	-	-	-	-					-	-
			-	-						
	Evening		-	-	Evening				Evening	

Minor species - Site W.

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Pres- ent	Feed- ing	Pres- ent	Feed- ing	Pres- ent	Feed- ing	Pres- ent	Feed- ing	Pres- ent	Feed- ing
1	Morning		-	-	Morning		-	-	Morning	
			-	-						
			-	-						
			-	-			Fog			
2			-	-						
	-	-								
			-	-						
	-	-	-	-	-	-				
3	1Go	1Go	-	-	-	-	-	-		
			-	-	2Go, 50K	2Go, 50K			-	-
	1Go	1Go	-	-	-	-	-	-		
	1Go	1Go	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-
	-	-	Evening		-	-	1L	-	-	-
	-	-			-	-			-	-
	-	-			-	-	Fog			
5	-	-			-	-			2M	-
	-	-			-	-			-	-
	-	-			-	-			-	-
	-	-			-	-			-	-
6					-	-			-	-
	-	-			-	-			-	-
	-	-			-	-	Evening		-	-
	-	-			-	-				

For key to species see overleaf.

Minor species - Site W (continued)

Hours after High Water	Numbers observed in study area									
	31/10/73		8/11/73		30/1/74		3/4/74		11/4/74	
	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding	Present	Feeding
7	-	-			-	-			-	-
	-	-	Morning		-	-			-	-
	-	-	-	-	-	-	Morning			
	-	-	1Cu	-	-	-				
8	-	-			-	-			-	-
	-	-	-	-	-	-			-	-
	-	-	-	-	-	-			-	-
	-	-	-	-	-	-			-	-
9	-	-			-	-			-	-
	-	-			-	-			-	-
	-	-	-	-	-	-	Fog		-	-
	-	-	-	-	-	-			-	-
10	-	-	-	-	-	-			-	-
	-	-	-	-	-	-			-	-
	-	-	-	-	-	-			-	-
	-	-	-	-	-	-			-	-
11	-	-	-	-	-	-			-	-
	-	-	-	-						
	-	-	-	-					-	-
	-	-	-	-					1Cu	-
12	-	-	-	-					-	-
	-	-	-	-					-	-
			-	-						
	Evening		-	-	Evening				Evening	

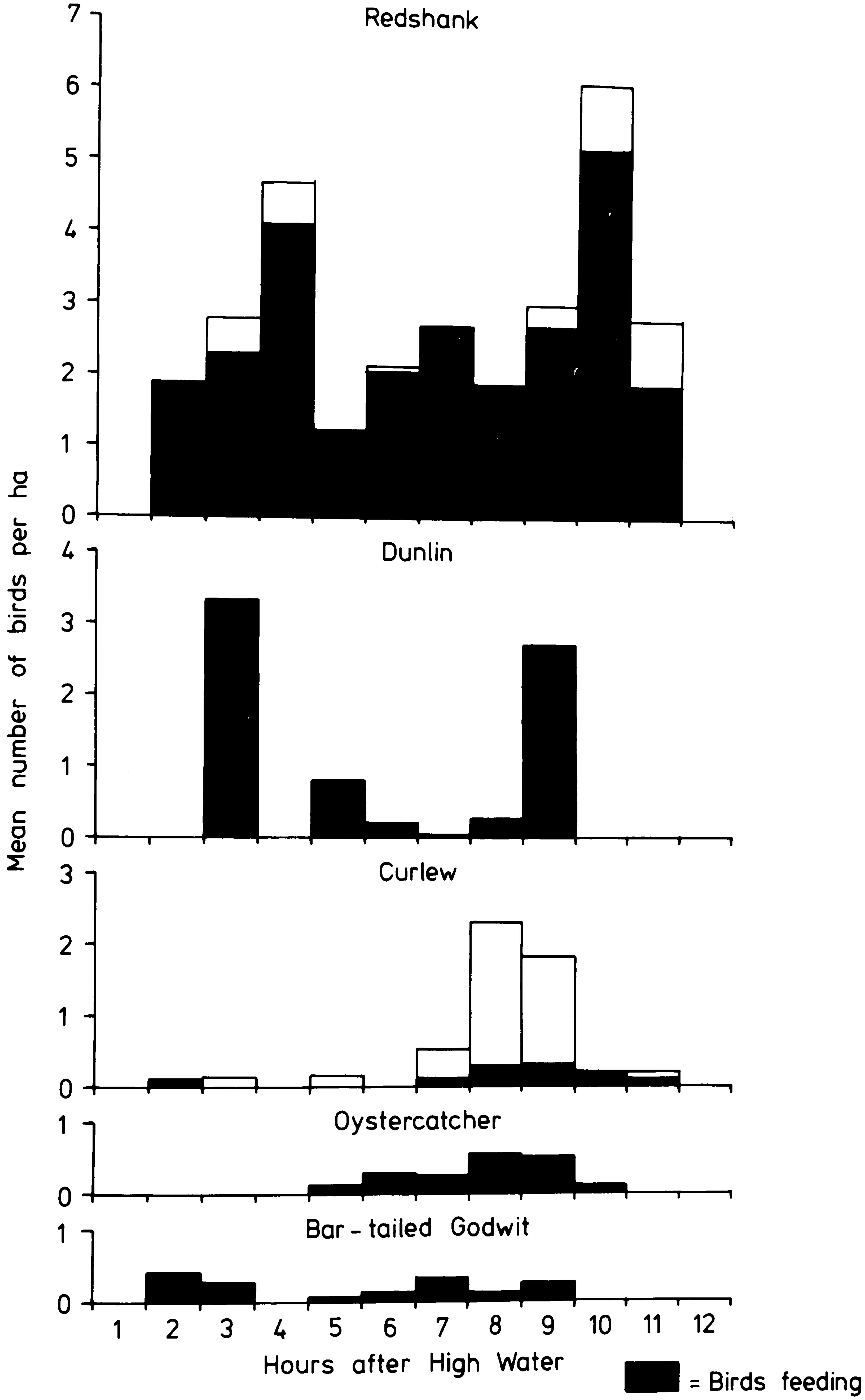
Go = Godwit K = Knot L = Lapwing

Cu = Curlew M = Mallard

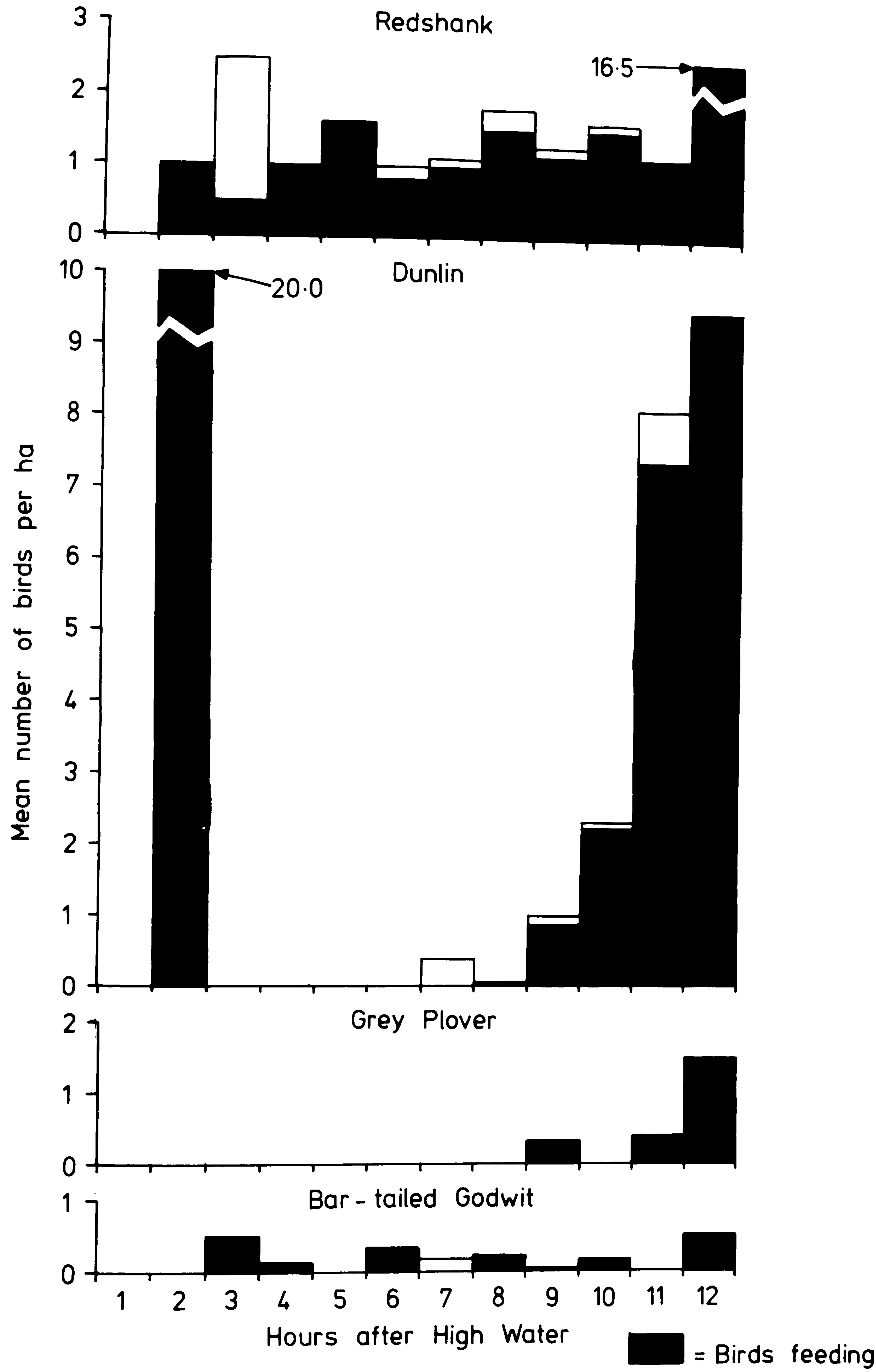
ii. Shorebird species associated with Spartina 1972/73.

Indices of Occurrence and Feeding 1972/73

Species	Site B I. of O.	Site B I. of F.	Site W I. of O.	Site W I. of F.
Redshank	29.31	25.99	30.65	27.82
Dunlin	7.39	7.39	41.37	40.05
Curlew	5.49	1.14	0.26	0.17
Bar-tailed Godwit	1.62	1.62	2.05	1.85
Oystercatcher	1.88	1.88	0.25	-
Grey Plover	1.14	0.72	2.20	2.20
Shelduck	-	-	-	-
Turnstone	0.28	-	-	-
Mallard	-	-	-	-
Teal	-	-	-	-
Knot	3.27	3.06	-	-
Lapwing	-	-	0.17	-



Seasonal mean densities of shorebirds present and feeding during one low tide cycle at Site B in 1972/73



Seasonal mean densities of shorebirds present and feeding during one low tide cycle at Site W in 1972/73

iii. Results of Redshank Predation Observations 1973/74.

Site B.

Hours after High Water	Mean feeding rate (Prey items taken/minute) of individual birds			
	31/10/73	8/11/73	3/4/74	11/4/74
1	-	-	-	
2	2.0,2.67,9.67	-	21.0,36.0,27.0	17.0,13.2,24.0, 17.5
3	6.0,6.25,11.0, 6.5,3.25	6.33,9.5,25.33	33.3,29.5,21.0, 29.67	8.0,13.3,16.5, 11.8
4	5.5,3.33,5.0	-	33.0,27.5,22.0	8.0,7.6
5	7.33,3.0,2.25, 4.0	-	-	7.8,9.5,11.0, 6.0,9.0,12.0
6	-	-	-	5.0,8.3,11.0, 11.0,10.0,13.75
7	5.0,3.33,8.5, 9.67	0,5.67,3.0	0,23.0	-
8	3.0,14.0,3.0	7.67,7.0,7.0, 6.33	14.0,27.0,18.0, 27.07,6.44,20.0	10.8,11.0
9	9.0,6.5	9.0,8.4,5.0, 10.0,7.0	11.0,20.2	7.0,6.5
10	12.0,8.0,7.5, 14.0	6.67,22.0, 12.2	16.0,22.6	3.5
11	12.5,10.0	-	22.0,16.0,23.7, 24.0,19.0	12.0,7.0,7.0, 5.5
12	-	-		

Site W.

Hours after High Water	Mean feeding rate (prey items taken/minute) of individual birds				
	31/10/73	8/11/73	30/1/74	3/4/74	11/4/74
1	-	-	-	-	-
2	-	-	-	-	-
3	19.3,7.0, 10.0,9.0.	1.67,16.0, 6.0.	25.0,8.0, 7.0,14.0.	4.0,26.0, 3.33,31.0, 0.	2.0,40.0.
4	14.0,13.0.	-	9.0,5.0, 9.0.	24.0,42.0, 1.5.	-
5	14.5	-	19.2,2.0, 7.2.	-	-
6	14.0	-	3.0.	-	56.0.
7	17.2,8.5.	-	18.0,7.0, 8.6,10.0, 7.5.	-	-
8	16.0,13.67, 13.5.	-	25.0,5.0, 10.5.	-	29.0,18.0.
9	3.5,6.5, 10.0.	-	4.0,5.33, 2.0,3.0.	-	6.8,1.0, 2.9,28.8, 4.0.
10	6.8,7.0, 3.33.	-	3.0.	-	3.0,3.0, 1.8,3.0, 2.0.
11	13.0,16.0, 8.0,28.0.	12.0	-	-	9.0,16.7, 7.7,5.7.
12	-	-	-	-	-

REFERENCES

ANDERSON, A. (1971) Intertidal activity, breeding and the floating habit of Hydrobia ulvae in the Ythan estuary. J. mar. biol. Ass. U.K., 51 : 423 - 37.

ARUDPRAGASAM, K.D. and NAYLOR, E. (1964a) Gill ventilation and the role of reversed respiratory currents in Carcinus maenas (L.). J. exp. Biol., 41 : 229 - 307.

ARUDPRAGASAM, K.D. and NAYLOR, E. (1964b) Gill ventilation volumes, oxygen consumption and respiratory rhythms in Carcinus maenas (L.). J. exp. Biol., 41 : 309 - 21.

BARBOSA, P. and PETERS, T.M. (1970) Dye-induced changes in the developmental physiology of Aedes aegypti larvae. Ent. exp. appl., 13 : 293 - 99.

BARNES, B.M. and BARNES, R.D. (1954) The ecology of the spiders of maritime drift lines. Ecology, 35 : 25 - 35.

BARNES, R.D. (1953) The ecological distribution of spiders in non-forest maritime communities at Beaufort, North Carolina. Ecol. Monogr., 23 : 315 - 37.

BATE, C.S. and WESTWOOD, J.O. (1868) A History of the British Sessile-eyed Crustacea. Vol. II. London.

BONGIORNO, S.F. (1970) Nest site selection by adult laughing gulls (Larus atricilla). Anim. Behav. 18 : 434 - 44.

BRADY, F. (1943) The distribution of the fauna of some intertidal sands and muds on the Northumberland coast. J. Anim. Ecol., 12 : 27 - 41.

BRADY, F. (1949) The fluctuations of some common shorebirds on the north Northumberland coast. Brit. Birds, 42 : 297 - 307.

BRAFIELD, A.E. (1964) The oxygen content of interstitial water in sandy shores. J. Anim. Ecol., 33 : 97 - 116.

BRAFIELD, A.E. and NEWELL, G.E. (1961) The behaviour of Macoma balthica. J. mar. biol. Ass. U.K., 41 : 81 - 7.

BRAYBROOKS, E.M. (195~~8~~7) The general ecology of Spartina townsendii ~~(sic. S. anglica)~~ with special reference to sward-build-up and degradation. Unpublished M.Sc. thesis, University of Southampton.

BUTCHER, R.W. (1941) The distribution of Zostera (Eelgrass, Wigeon Grass) and other seashore plants in relation to migrations of wild-fowl. International Wildfowl Inquiry. Vol. I. Ch.III, p. 29 - 49.

CAMERON, G.N. (1972) Analysis of insect trophic diversity in two salt-marsh communities. Ecology, 53 : 58 - 73.

CAPSTICK, C.K. (1957) The salinity characteristics of the middle and upper reaches of the River Blyth Estuary. J. Anim. Ecol., 26 : 295 - 315.

CHAPMAN, A. (1907) Bird life of the Borders. 2nd Edition. Gurney & Jackson, London & Edinburgh.

CHATER, E.H. and JONES, H. (1957) Some observations of Spartina townsendii in the Dovey estuary. J. Ecol., 45 : 157 - 67.

CONDREY, R.E., GOSSELINK, J.G., and BENNET, H.J. (1972) Comparison of the assimilation of different diets by Penaeus setiferus and P. aztecus. U.S. Natl. Mar. Fish. Serv. Fish. Bull., 70 : 1281 - 92.

DAVIS, L.V. and GRAY, I.E. (1966) Zonal and seasonal distribution of insects in North Carolina salt marshes. Ecol. Monogr., 36 : 275 - 95.

DELAGE, Y. (1881) Contribution à l'Étude de l'appareil circulatoire des Crustaces Edriophthalmes Marins. Archives de Zoologie Exp. et Gen., 9 : 1 - 173.

DRINNAN, R.E. (1957) The winter feeding of the oystercatcher, (*Haematopus ostralegus*) on the edible cockle (*Cardium edule*). J. Anim. Ecol., 26 : 441 - 69.

DUNCAN, A. (1960) The spawning of *Arenicola marina* (L.) in the British Isles. Proc. zool. Soc. Lond., 134 : 137 - 56.

DUNN, E.K. (1967) The distribution of Macoma balthica on the Ythan Estuary, Aberdeenshire. Unpublished undergraduate thesis, University of Aberdeen.

ELTRINGHAM, S.K. (1971) Life in Mud and Sand. English Universities Press, London.

EVANS, P.R. (1974a) The effects of stage I of the reclamation of Seal Sands on the invertebrate and bird populations. Report to the Teesmouth Bird Club (mimeographed).

EVANS, P.R. (1974b) The effects of partial reclamation of Seal Sands, Teesmouth, on the bird populations, January - September 1974. Report to the Royal Society for the Protection of Birds (mimeographed).

FENCHEL, T.M., and RIEDL, R.J. (1970) The sulfide system: a new biotic community underneath the oxidised layer of marine sand bottoms. Mar. Biol. (Berlin) 7 : 255 - 68.

FRASER, J.H. (1932) Observations on the fauna and constituents of an estuarine mud in a polluted area. J. mar. biol. Ass. U.K., 18 : 69 - 85.

GEE, J.M. (1961) Ecological studies in South Benfleet Creek, with special reference to the amphipod genus *Corophium*. Essex Nat., 30 : 291 - 309.

GIBBS, P.E. (1968) Observations on the population of *Scoloplos armiger* at Whitstable. J. mar. biol. Ass. U.K., 48 : 225 - 54.

GOETHE, F. (1969) Zur Einwanderung der Lachmöwe, Larus ridibundus, in das Gebiet der deutschen Nordseeküste und ihrer Inseln. Bonn. zool. Beitr., 20 : 164 - 70.

GOODMAN, P.J. (1959) The possible role of pathogenic fungi in die-back of Spartina townsendii. Trans. Brit. Mycol. Soc., 42 : 409 - 15.

GOODMAN, P.J. (1960) Investigations into 'die-back' in Spartina townsendii Agg. II. The morphological structure and composition of the Lymington sward. J. Ecol., 48 : 711 - 24.

GOODMAN, P.J., BRAYBROOKS, E.M. and LAMBERT, J.M. (1959) Investigations into 'die-back' in Spartina townsendii Agg. I. The present status of Spartina townsendii in Britain. J. Ecol., 47 : 651 - 77.

GOODMAN, P.J. and WILLIAMS, W.J. (1961) Investigations into 'die-back' in Spartina townsendii Agg. III. Physiological correlates of 'die-back'. J. Ecol., 49 : 391 - 8.

GOSS-CUSTARD, J.D. (1969) The winter feeding ecology of the redshank Tringa totanus. Ibis, 111 : 338 - 56.

GOSS-CUSTARD, J.D. (1970) The responses of redshank (Tringa totanus (L.)) to spatial variations in the density of their prey. J. Anim. Ecol., 39 : 91 - 113.

GOSS-CUSTARD, J.D. (1973) Current problems in studying the feeding ecology of estuarine birds. Coastal Ecology Research Paper, No. 4 : The Nature Conservancy, Norwich.

GOSS-CUSTARD, J.D. and JONES, R.E. (in press) The diet of Redshank Tringa totanus and Curlew Numenius arquata on the Wash from observations and analyses of pellets. Bird Study.

GREEN, J. (1968) The Biology of Estuarine Animals. Sidgwick and Jackson, London.

GREENWOOD, J.J.D., and GOSS-CUSTARD, J.D. (1970) The relative digestibility of the prey of Redshank _Tringa totanus_. _Ibis_, _112_ : 543 - 4.

HART, T.J. (1930) Preliminary notes on the bionomics of the Amphipod, _Corophium volutator_ Pallas. _J. mar. biol. Ass. U.K._, _16_ : 761 - 90.

HARTLEY, P.H.T. (1948) The assessment of the food of birds. _Ibis_, _90_ : 361 - 81.

HEARD, R.W. III. (1970) Parasites of the Clapper Rail, _Rallus longirostris_ Boddaert II. Some trematodes and cestodes from _Spartina_ marshes of the eastern United States. _Proc. Helminthol. Soc. Wash._, _37_ : 147 - 53.

HECHT, F. (1932) Der chemische Einfluss organischer Zersetzungsstoffe auf das Benthos, dargelegt an Untersuchungen mit marinen Polychaeten, insbesondere _Arenicola marina_ L. _Senkenbergiana_, _14_ : 199 - 220.

HELLER, J. (1975) The taxonomy of some British _Littorina_ species, with notes on their reproduction. _Zool. J. Linn. Soc._, _56_ : 131 - 51.

HEPPLESTON, P.R. (1971) The feeding ecology of oystercatchers (_Haematopus ostralegus_ L.) in winter in Northern Scotland. _J. Anim. Ecol._, _40_ : 651 - 72.

HOLME, N.A. and McINTYRE, A.D. (1971) Methods for the Study of Marine Benthos. _IBP Handbook_, _No. 16_, pp 35 - 6.

HOWIE, D.I.D. (1959) The spawning of _Arenicola marina_ (L.) I. The breeding season. _J. mar. biol. Ass. U.K._, _38_ : 395 - 406.

HUBBARD, C.E. (1968) _Grasses_. Penguin, Harmondsworth.

HUBBARD, J.C.E. and STEBBINGS, R.E. (1967) Distribution, dates of origin and acreage of _Spartina townsendii_ (_sensu lato_) marshes in Great Britain. _Proc. Bot. Soc. Br. Isl._, _7_ : 1 - 7.

HUSKINS, C.L. (1930) The origin of *Spartina townsendii*. *Genetica*, *12*: 531 - 8.

HYNES, H.B.N. (1950) The food of freshwater Sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*) with a review of methods used in studies of the food of fishes. *J. Anim. Ecol.*, *19* : 36 - 58.

JØRGENSEN, C.B. (1966) Environmental factors influencing feeding activity. In: *Biology of Suspension Feeding*, pp. 104 - 9, Pergamon, Oxford.

KERWIN, J.A. (1971) Distribution of the fiddler crab (*Uca minax*) in relation to marsh plants within a Virginia estuary. *Chesapeake Sci.*, *12* : 180 - 3.

KERWIN, J.A. (1972) Distribution of the salt marsh snail (*Melampus bidentatus* Say) in relation to marsh plants in the Poropotank River area, Virginia. *Chesapeake Sci.*, *13* : 150 - 3.

KOERSVELD, E. van (1951) Difficulties in stomach analysis. *Proc. X Int. orn. Congr. Uppsala* : 592 - 4.

KUENZLER, E.J. (1961) Structure and energy flow of a mussel population in a Georgia salt marsh. *Limnol. Oceanogr.*, *6* : 191 - 204.

LADLE, M. (1966) *Studies on the Biology of the Macrofauna of Budle Bay, Northumberland*. Unpublished Ph.D. thesis, University of Newcastle.

LAMBERT, J.M. (1964) The *Spartina* story. *Nature*, *204* : 1136 - 8.

LLOYD, A.J. and YONGE, C.M. (1947) The biology of *Crangon vulgaris* L. in the Bristol Channel and Severn Estuary. *J. mar. biol. Ass. U.K.*, *26* : 626 - 61.

LOOSANOFF, V.L. and DAVIS, H.C. (1947) Staining of oyster larvae as a method for studies of their movements and distribution. *Science*, *106* : 597 - 8.

LUXTON, M. (1964) Some aspects of the biology of saltmarsh Acarina. Acaralogia, C.R. 1er Congrès Int. d'Acaralogie, Fort Collins, Colorado, U.S.A.: 172 - 82.

MACDONALD, K.B. (1969) Quantitative studies of salt marsh mollusc faunas from the North American Pacific coast. Ecol. Monogr., 39 : 33 - 60.

McLUSKY, D.S. (1967) Some effects of salinity on the survival, moulting and growth of Corophium volutator (Amphipoda). J. mar. biol. Ass. U.K., 47 : 607 - 17.

McLUSKY, D.S. (1968) Some effects of salinity on the distribution and abundance of Corophium volutator in the Ythan Estuary. J. mar. biol. Ass. U.K., 48 : 443 - 54.

McMAHAN, E.A., KNIGHT, R.L., and CAMP, A.R. (1972) A comparison of microarthropod populations in sewage-exposed and sewage-free Spartina salt marshes. Environ. Entomol., I : 244 - 52.

McMILLAN, N.F. (1948) Possible biological races in Hydrobia ulvae (Pennant) and their varying resistance to lowered salinity. J. Conch., 23 : 14 - 16.

MANN, F.G. and SAUNDERS, B.C. (1960) Practical Organic Chemistry. 4th Edition. Longman, London.

MARCHANT, C.J. (1963) Corrected chromosome numbers for Spartina x townsendii and its parent species. Nature, 199 : 229.

MARCHANT, C.J. (1967) Evolution in Spartina (Gramineae) I. The history and morphology of the genus in Britain. J. Linn. Soc. (Bot.), 60 : 1 - 24.

MARCHANT, C.J. (1968a) Evolution in Spartina (Gramineae) II. Chromosomes, basic relationships and the problem of S. x townsendii Agg. J. Linn. Soc. (Bot.), 60 : 381 - 409.

MARCHANT, C.J. (1968b) Evolution in Spartina (Gramineae) III. Species chromosome numbers and their taxonomic significance. J. Linn. Soc. (Bot.), 60 : 411 - 7.

MARPLES, T.C. (1966) A radionuclide tracer study of arthropod food chains in a Spartina salt marsh ecosystem. Ecology, 47 : 270 - 7.

MARPLES, T.C. and ODUM, E.P. (1964) A radionuclide tracer study of arthropod food chains in a Spartina alterniflora salt marsh. Bull. Ecol. Soc. Am., 45 : 81.

MEADOWS, P.S. (1964a) Substrate selection by Corophium species : the particle size of substrates. J. Anim. Ecol., 33 : 387 - 94.

MEADOWS, P.S. (1964b) Experiments on substrate selection by Corophium species : films andbacteria on sand particles. J. exp. Biol., 41 : 499 - 511.

MEADOWS, P.S. (1964c) Experiments on substrate selection by Corophium volutator (Pallas) : depth selection and population density. J. exp. Biol., 41 : 677 - 87.

MEADOWS, P.S. (1967) Discrimination, previous experience and substrate selection by the amphipod Corophium. J. exp. Biol., 47 : 553 - 9.

MEADOWS, P.S. and REID, A. (1966) The behaviour of Corophium volutator (Crustacea : Amphipoda). J. Zool., Lond., 150 : 387 - 99.

MEYER, A.N. (1973) An investigation into certain aspects of the ecology of Fenham Flats and Budle Bay, Northumberland. Unpublished M.Sc. thesis, University of Durham.

MORGAN, E. (1965) The activity of the amphipod Corophium volutator (Pallas) and its possible relationship to changes in hydrostatic pressure associated with the tides. J. Anim. Ecol., 34 : 731 - 46.

MORGANS, J.F.C. (1956) Notes on the analysis of shallow-water soft substrata. J. Anim. Ecol., 25 : 367 - 87.

MULICKI, Z. (1957) Ecology of the more important Baltic Invertebrates. Reports of the Sea Fisheries Institute in Gdynia, No. 9, pp 313 - 7.

MUUS, B.J. (1963) Some Danish Hydrobiidae with the description of a new species, Hydrobia neglecta. Proc. malacol. Soc. Lond., 35 : 131 - 8.

NAYLOR, E. (1958) Tidal and diurnal rhythms of locomotory activity in Carcinus maenas (L.). J. exp. Biol., 35 : 602 - 10.

NAYLOR, E. (1960) Locomotory rhythms in Carcinus maenas from non-tidal conditions. J. exp. Biol., 37 : 481 - 8.

NEW, J.G. (1958) Dyes for studying the movements of small mammals. J. Mammal., 39 : 416 - 29.

NEWELL, G.E. (1948) A contribution to our knowledge of the life history of Arenicola marina L. J. mar. biol. Ass. U.K., 27 : 554 - 80.

NEWELL, G.E. (1958) An experimental analysis of the behaviour of Littorina littorea (L.) under natural conditions and in the laboratory. J. mar. biol. Ass. U.K., 37 : 241 - 66.

NEWELL, R.C. (1962) Behavioural aspects of the ecology of Peringia (= Hydrobia) ulvae (Pennant) (Gastropoda, Prosobranchia). Proc. zool. Soc. Lond., 138 : 49 - 75.

NEWELL, R.C. (1965) The role of detritus in the nutrition of two marine deposit feeders, the prosobranch Hydrobia ulvae and the bivalve Macoma balthica. Proc. zool. Soc. Lond., 144 : 25 - 45.

NEWELL, R.C. (1972) Biology of Intertidal Animals. Revised edition. Unwin, London.

NEWTON, I. (1967) The adaptive radiation and feeding ecology of some British finches. Ibis, 109 : 33 - 98.

NORTON-GRIFFITHS, M. (1966) Oystercatchers and mussels. Ibis, 108 : 455 - 6.

ODUM, E.P. and SMALLEY, A.E. (1959) Comparison of population energy flow of a herbivorous and a deposit-feeding invertebrate in a salt marsh ecosystem. Proc. Nat. Acad. Sci. U.S.A., 45 : 617 - 22.

ODUM, E.P. and de la CRUZ, A.A. (1967) Particulate organic detritus in a Georgia salt marsh estuarine ecosystem. Amer. Ass. Advan. Sci. Publ., 83 : 383 - 8.

OLIVER, F.W. (1920) Spartina problems. Ann. appl. Biol., 7 : 57.

OLNEY, P.J.S. (1963) The food and feeding habits of the teal Anas creca L., Proc. zool. Soc. Lond., 140 : 169 - 210.

PACKHAM, J.R. and LIDDLE, M.J. (1970) The Cefni salt marsh, Anglesey, and its recent development. Field Study, 3 : 331 - 56.

PAYNE, K. (1972) A survey of the Spartina-feeding insects in Poole Harbour, Dorset. Entomol. mon. Mag., 108 : 66 - 79.

PERKINS, E.J. (1957) The blackened sulphide-containing layer of marine soils, with special reference to that found at Whitstable, Kent. Ann. Mag. nat. Hist., 10 : 25 - 35.

PERKINS, E.J. (1958) The food relationships of the microbenthos, with particular reference to that found at Whitstable, Kent. Ann. Mag. nat. Hist. Ser. 13, vol. 1 : 64 - 77.

PERRY, R. (1946) A Naturalist on Lindisfarne. Lindsay Drummond, London.

PETERS, T.M. and CHEVONE, B.I. (1968) Marking Culex pipiens Linn. larvae with vital dyes for larval ecological studies. Mosq. News, 28 : 24 - 8.

PRATER, A.J. (1972a) The ecology of Morecambe Bay III. The food and feeding habits of Knot (Calidris canutus L.) in Morecambe Bay. J. appl. Ecol., 9 : 179 - 94.

PRATER, A.J. (1972b) Food of Turnstones in Morecambe Bay. Bird Study, 19 : 51 - 2.

RANWELL, D.S. (1964a) Spartina salt marshes in southern England. II. Rate and seasonal pattern of sediment accretion. J. Ecol., 52 : 79 - 94.

RANWELL, D.S. (1964b) Spartina salt marshes in southern England. III. Rates of establishment, succession and nutrient supply at Bridgewater Bay, Somerset. J. Ecol., 52 : 95 - 105.

RANWELL, D.S. (1967) World resources of Spartina townsendii (sensu lato) and economic use of Spartina marshland. J. appl. Ecol., 4 : 239 - 56.

RANWELL, D.S. (1972) Ecology of Salt Marshes and Sand Dunes. Chapman and Hall, London. pp 258.

RANWELL, D.S. and DOWNING, B.M. (1959) Brent goose (Branta bernicla (L.)) winter feeding pattern and Zostera resources at Scolt Head Island, Norfolk. Anim. Behav., 7 : 42 - 56.

RANWELL, D.S., BIRD, E.C.F., HUBBARD, J.C.E. and STEBBINGS, R.E. (1964) Spartina salt marshes in Southern England. V. Tidal emergence and chlorinity in Poole Harbour. J. Ecol., 52 : 627 - 41.

REED, A., and MOISAN, G. (1971) The Spartina tidal marshes of the St. Lawrence estuary and their importance to aquatic birds. Naturaliste can., 98 : 905 - 22.

SANDISON, E.E. (1966) The oxygen consumption of some intertidal gastropods in relation to zonation. J. zool. Lond., 149 : 163 - 73.

SANDISON, E.E. (1967) Respiratory response to temperature and temperature tolerance of some intertidal gastropods. J. exp. mar. Biol. Ecol., 1 : 271 - 81.

SCHLIEPER, C. (1929) Über die Einwirkung niederer Salzkonzentrationen auf marine Organismen. Z. vergl. Physiol., 9 : 478 - 514.

SHANNON, C.E. and WEAVER, W. (1963) The Mathematical Theory of Communication. University of Illinois Press, Urbana.

SIVANESAN, A. and MANNERS, J.G. (1970) Fungi associated with Spartina townsendii in healthy and 'die-back' sites. Trans. Brit. mycol. Soc., 55 : 191 - 204.

SIVANESAN, A. and MANNERS, J.G. (1972) Bacteria of muds colonised by Spartina townsendii and their possible role in Spartina die-back. Plant Soil, 36 : 349 - 61.

SMALLEY, A.E. (1959) The role of two invertebrate populations, Littorina irrorata and Orchelimum fidicinium, in the energy flow of a salt marsh ecosystem. Unpublished Ph.D. thesis, University of Georgia.

SMALLEY, A.E. (1960) Energy flow of a salt marsh grasshopper population. Ecology, 41 : 672 - 7.

SMITH, P.C. (1975) A study of the winter feeding ecology and behaviour of the Bar-tailed Godwit Limosa lapponica. Unpublished Ph.D. thesis, University of Durham.

SMITH, P.C. and EVANS P.R. (1973) Studies of shorebirds at Lindisfarne, Northumberland. 1. Feeding ecology and behaviour of the Bar-tailed Godwit. Wildfowl, 24 : 135 - 9.

SMITH, R.I. (1955a) On the distribution of Nereis diversicolor in relation to salinity in the vicinity of Tvärminne, Finland, and the Isefjord, Denmark. Biol. Bull. mar. biol. Lab. Woods Hole, 108 : 326 - 45.

SMITH, R.I. (1955b) Salinity variation in interstitial water at Kames Bay, Millport, with reference to the distribution of Nereis diversicolor. J. mar. biol. Ass. U.K., 34 : 33 - 46.

SMITH, R.I. (1956) The ecology of the Tamar Estuary. VII. Observations on the interstitial salinity of intertidal muds in the estuarine habitat of Nereis diversicolor. J. mar. biol. Ass. U.K., 35 : 81 - 104.

SOUTHWARD, A.J. (1953) The fauna of some sandy and muddy shores in the south of the Isle of Man. Proc. Trans. Liv. Biol. Soc., 59 : 51 - 71.

STEPHEN, A.C. (1930) Studies on the Scottish marine fauna : Additional observations on the fauna of the sandy and muddy areas of the tidal zone. Trans. roy. Soc. Edinb., 56 : 521 - 35.

STOPFORD, S.C. (1951) An ecological survey of the Cheshire foreshore of the Dee Estuary. J. Anim. Ecol., 20 : 103 - 22.

STRICKLAND, J.D.H. and PARSONS, T.R. (1960) A Manual of seawater analysis. Fish. Res. Board Can., Bull., 125 : 19 - 21.

TEAL, J.M. (1958) Distribution of fiddler crabs in Georgia salt marshes. Ecology, 39 : 185 - 93.

TINSLEY, J. (1950) The determination of organic carbon in soils by dichromate mixtures. Trans. 4th Inst. Congr. Soil Sci., 1 : 161 - 6.

TRAMER, E.J. (1969) Bird species diversity : Components of Shannon's formula. Ecology, 50 : 927 - 9.

VADER, W.J.M. (1964) A preliminary investigation into the reactions of the infauna of the tidal flats to tidal fluctuations in water level. Neth. J. Sea Res., 2 : 189 - 222.

VAN BENTHEM JUTTING, W.S.S. (1959) Ecology of the brackish water Mollusca in the Netherlands. Basteria, 23 : 77 - 105.

WATKIN, E.E. (1941) The yearly life cycle of the amphipod Corophium volutator. J. Anim. Ecol., 10 : 77 - 93.

WEBB, D.A. (1940) Ionic regulation in Carcinus maenas. Proc. Roy. Soc. B., 129 : 107 - 36.

WEBB, J.E. (1958) The ecology of Lagos Lagoon V. Some physical properties of lagoon deposits. Phil. Trans. Roy. Soc., B., 241 : 393 - 419.

WILSON, C.E. (1969) Accretion and the spread of Spartina on the foreshore of Lytham St. Annes, Lancashire. Unpublished M.Sc. thesis, University of Lancaster.

WOOD, J.B. (1972) Aspects of the ecology of Hydrobia ulvae. Unpublished M.Sc. thesis, University of Durham.